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# *Anchisaurus polyzelus* (Hitchcock): The Smallest Known Sauropod Dinosaur and the Evolution of Gigantism among Sauropodomorph Dinosaurs

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## Abstract

A review of the type and referred specimens of *Anchisaurus polyzelus* (Hitchcock) and *Ammosaurus major* Marsh, from the Early Jurassic Portland Formation (Hartford Basin, Newark Supergroup), indicates that the latter is a junior synonym of the former. The material displays derived similarities with sauropod dinosaurs that are not present in their sister group, the prosauropods. Cladistic analysis strongly supports the hypothesis that *Anchisaurus polyzelus* is the most basal known member of Sauropoda. Thus *A. polyzelus* becomes the smallest known sauropod. Optimization of femur length using square change parsimony indicates that the lineage leading to Neosauropoda underwent gradual and sustained size increase for most of its history since its divergence from Theropoda. It also shows that *A. polyzelus* represents a reversal of this trend and has decreased in size relative to the sauropod common ancestor.

## Keywords

*Anchisaurus*, Prosauropoda, Sauropoda, cladistic analysis, gigantism.

## Abbreviations

|       |  |
|-------|--|
| AM    | Amherst College Museum, Amherst, Massachusetts                                       |
| BP    | Bernard Price Institute, University of the Witwatersrand, Johannesburg, South Africa |
| BRSMG | Bristol City Museum and Art Galleries, Bristol, United Kingdom                       |
| BRUG  | Department of Earth Sciences, University of Bristol, Bristol, United Kingdom         |
| GPIT  | Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany |
| HMN   | Museum für Naturkunde der Humboldt Universität, Berlin, Germany                      |
| MCP   | Museu de Ciências e Tecnologia, Pontificia Universidade Católica                     |

|      |  |      |                                   |
|------|--|------|-----------------------------------|
|      | do Rio Grande do Sul,<br>Porto Alegre, Brazil  | ds   | dorsosacral vertebra              |
| MNA  | Museum of Northern Arizona,<br>Flagstaff, Arizona  | emf  | external mandibular fenestra      |
| MOR  | Museum of the Rockies,<br>Bozeman, Montana   | exop | exoccipital–opisthotic complex    |
| NM   | National Museum,<br>Bloemfontein, South Africa   | f    | foramen                           |
| PULR | Museo de Paleontología,<br>Universidad Provincial de<br>La Rioja, La Rioja, Argentina              | fi   | fibula                            |
| PVL  | Fundación Miguel Lillo,<br>Universidad Nacional de<br>Tucumán, San Miguel de<br>Tucumán, Argentina | fin  | foramen magnum                    |
| SAM  | South African Museum,<br>Capetown, South Africa  | g    | glenoid                           |
| SMNS | Staatliches Museum für<br>Naturkunde, Stuttgart, Germany   | ic   | internal carotid foramen          |
| TATE | Tate Geological Museum,<br>Casper College,<br>Casper, Wyoming                                      | ifen | intracostal fenestra              |
| UCMP | University of California<br>Museum of Paleontology,<br>Berkeley, California                        | ip   | iliac peduncle                    |
| YPM  | Peabody Museum of<br>Natural History, Yale University,<br>New Haven, Connecticut                   | j    | jugal                             |
|      |  | l    | lacrimal                          |
|      |  | mx   | maxilla                           |
|      |  | oc   | occipital condyle                 |
|      |  | p    | lateral pit                       |
|      |  | pa   | pubic apron                       |
|      |  | pb   | pubic boot                        |
|      |  | po   | postorbital                       |
|      |  | psr  | parasphenoid rostrum              |
|      |  | q    | quadrate                          |
|      |  | rc   | radial condyle                    |
|      |  | rsaf | rostral surangular foramen        |
|      |  | s1   | first primordial sacral vertebra  |
|      |  | s2   | second primordial sacral vertebra |
|      |  | sa   | surangular foramen                |
|      |  | saf  | caudal surangular foramen         |
|      |  | so   | supraoccipital                    |
|      |  | sr   | sacral rib                        |
|      |  | t    | tooth                             |
|      |  | ti   | tibia                             |
|      |  | uc   | ulnar condyle                     |

*Abbreviations used in figures:*

|      |                                      |
|------|--------------------------------------|
| a    | angular                              |
| aof  | antorbital fossa                     |
| as   | astragalus                           |
| bo   | basioccipital                        |
| bpt  | basipterygoid process                |
| bsps | basisphenoid–parasphenoid<br>complex |
| bt   | basal tuber                          |
| c    | calcaneum                            |
| clp  | caudolateral process                 |
| crlp | cranio-lateral process               |
| d    | dentary                              |

## Introduction

Sauropod dinosaurs include the largest known terrestrial animals. Unfortunately, their early evolution and the sequence in which they acquired their specialized characteristics is poorly known. The record of definitive sauropods begins with *Isanosaurus attavipachi* in the latest Triassic (Buffetaut and others 2000). This

taxon is fragmentary and little can be said of its morphology. The earliest Jurassic sauropod, *Vulcanodon*, had acquired specializations such as large size (femur length exceeding 1 m), columnar limbs, elongated forelimbs, reduced muscular processes on the limb bones and a shorter metapodium with more robust lateral and medial elements (Wilson and Sereno 1998; Upchurch 1998; and Wilson 2002). These specializations are clearly adaptations for resisting the extreme loadings that bodyweights of at least several thousand kilograms place on the limbs and for graviportal locomotion. Among Dinosauria the closest relatives of the Sauropoda are, with little doubt, the assemblage of primitive taxa known as prosauropods. Although the name "prosauropod" is commonly used, it would be better to describe the whole assemblage as nonsauropod sauropodomorphs, given that Prosauropoda has been given a precise phylogenetic definition (the clade containing all taxa sharing a more recent common ancestor with *Plateosaurus engelhardti* than with *Saltasaurus loricatus*; Sereno 1998).

Understanding of the origin of Sauropoda hinges on determining the precise relationship between nonsauropod sauropodomorphs and the sauropods themselves. A recent analysis has found support for the hypothesis that the traditional prosauropod assemblage forms a pectinate array of forms along the stem of the Sauropoda (Yates 2003a). In this arrangement the true Prosauropoda is minimally inclusive (that is, it contains *Plateosaurus engelhardti* alone), and several robust taxa, such as *Melanorosaurus readi* and *Blikanasaurus cromptoni*, form

serially closer outgroups to the typical giant sauropods. Thus, the evolution of the sauropods involved a gradual and steady increase in size. In contrast, all other cladistic analyses of sauropodomorph relationships published to date (Upchurch 1995; Sereno 1999; Benton and others 2000) have found a maximally inclusive Prosauropoda (all sauropodomorphs that were not typical giant sauropods were found to be prosauropods). In this arrangement Sauropoda has a long ghost range over which their many specializations, including gigantic size, must have been acquired, possibly in a rapid burst before the beginning of the Jurassic when the first gigantic, graviportal sauropods appear. In both scenarios sauropod size increased at a steady pace after graviportal gigantism was achieved and can be seen in the stepwise increase in size of the basalmost branches of the graviportal clade (*Vulcanodon*, with a femur length of approximately 1100 mm, *Shunosaurus*, with a femur length of 1200 mm, *Barapasaurus*, with a femur length of 1310 mm [data from Wilson and Sereno 1998]).

The small, slender *Anchisaurus polyzelus* (Hitchcock 1865) is known from two localities in the Early Jurassic Portland Formation (Hartford Basin, Newark Supergroup). It was possibly facultatively bipedal (Galton 1976) and is nearly always considered to be a member of the Prosauropoda (Huene 1932; Romer 1956; Steel 1970; Galton 1976, 1990; Upchurch 1995; Sereno 1999; Benton and others 2000). The long-familiar species is known from relatively complete remains (Galton 1976). Nevertheless, its position within Prosauropoda varies considerably among

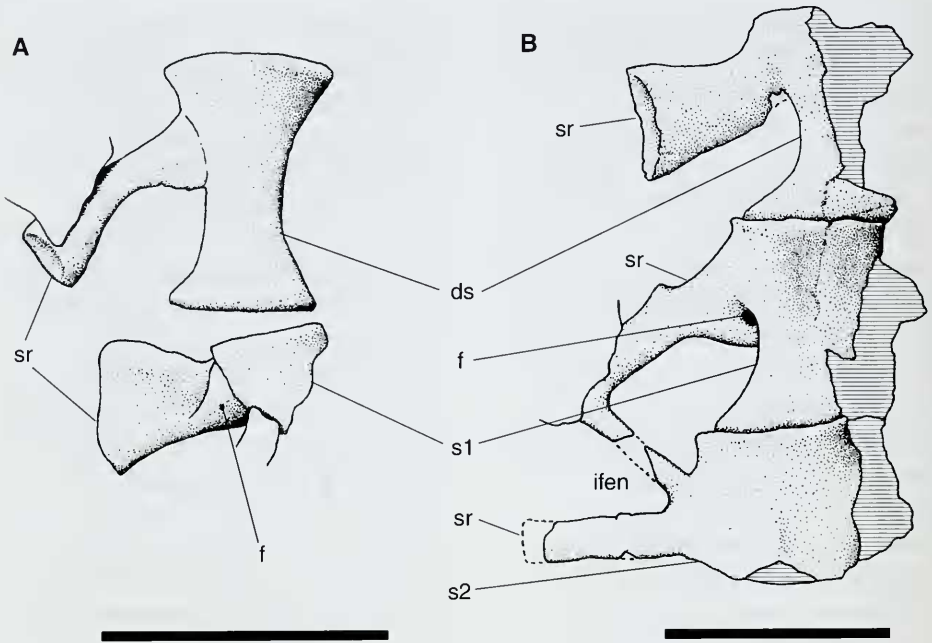


Figure 1

*Anchisaurus polyzelus*. A, YPM 1883, ventral view of sacrum; B, YPM 208, ventral view of sacrum. Scale 50 mm.

recent cladistic analyses. It has been placed as a basal member of the prosauropod clade (Upchurch 1995), as a sister group to the Melanorosauridae (Benton and others 2000; Galton and Upchurch, in press) and as the sister group of the Plateosauria (Serenó 1999). In Yates's analysis (2003a), in which the traditional Prosauropoda was broken into a paraphyletic array, *A. polyzelus* fell somewhere in the middle of this array, but its exact position differed among the various most-parsimonious trees. To resolve the source of these conflicting phylogenetic signals, the material was re-examined. Surprisingly, it was found that *A. polyzelus* shares with the gigantic sauropod dinosaurs several

derived characteristics that have not been previously recognized.

A second sauropodomorph taxon from the Portland Formation, *Ammosaurus major* Marsh (1889) (see also Marsh 1885), is usually regarded as distinct from *Anchisaurus polyzelus* following the work of Galton (1976), although Sereno (1999) considered them synonymous.

This paper supports the case for the synonymy of *Ammosaurus major* with *Anchisaurus polyzelus*, and for the taxon's phylogenetic position as the most basal known sauropod. The implications of this hypothesis for our understanding of sauropodomorph evolution is also examined.





Figure 2

*Anchisaurus polyzelus*, YPM 208, cross section through the distal ischia. Note that the postmortem separation of the left and right ischia has been corrected for. Scale 20 mm.

### Synonymy of *Ammosaurus major* with *Anchisaurus polyzelus*

The holotype of *Ammosaurus major* is a partial skeleton (YPM 208) recovered from the same quarry that yielded the most complete referred specimen of *Anchisaurus polyzelus*, YPM 1883 (Galton 1976; Weishampel and Young 1996). These two specimens share the following apomorphies, which are otherwise absent in closely related sauropodomorphs: a foramen opening ventrally at the base of the second sacral rib (Figure 1); an elongate preacetabular blade of the ilium that is more than twice as long as it is deep at its base (also in *Kotasaurus yamanpalliensis*, Yadagiri 2001); pubic obturator fenestrae that occupy most of the obturator plate; and flattened coplanar ischial shafts (also in many Neosauropoda; see Wilson and Sereno 1998, and Figure 2). The last character is also present in the holotype of *Anchisaurus polyzelus* (AM 41/109) and the juvenile specimen (YPM 209) that was referred to *Ammosaurus major* by Galton (1976).

The main character used by Galton (1976) to separate *Ammosaurus* from *Anchisaurus* was the broader foot of the

former. However, the proximal width to total length ratios (measured as the maximum dimension across all five metatarsals when in natural articulation) of the metatarsi of YPM 208, 1883 and 209 are similar (0.66, 0.62 and 0.60 respectively), and the differences are attributable to the size difference between the specimens (lengths of metatarsal 3 in the three specimens are 120, 98 and 48 mm, respectively; data from Galton 1976). Smaller specimens of other early sauropodomorph taxa show relatively narrower feet than fully adult specimens (for example, *Massospondylus carinatus* [Cooper 1981]). Other differences noted by Galton (1976) include a longer laterodistal groove on the tibia in YPM 208 and an open obturator notch in the pubis of YPM 1883. The first of these is probably a result of the severe craniocaudal crushing that the tibia of YPM 208 has undergone, whereas the second is probably due to the postmortem loss of the thin, caudomedial rim of the obturator fenestra. Loss of this rim is a common preservational defect of sauropodomorph pubes.

In conclusion, all sauropodomorph specimens from Manchester Quarry, as well as the holotype of *Anchisaurus poly-*

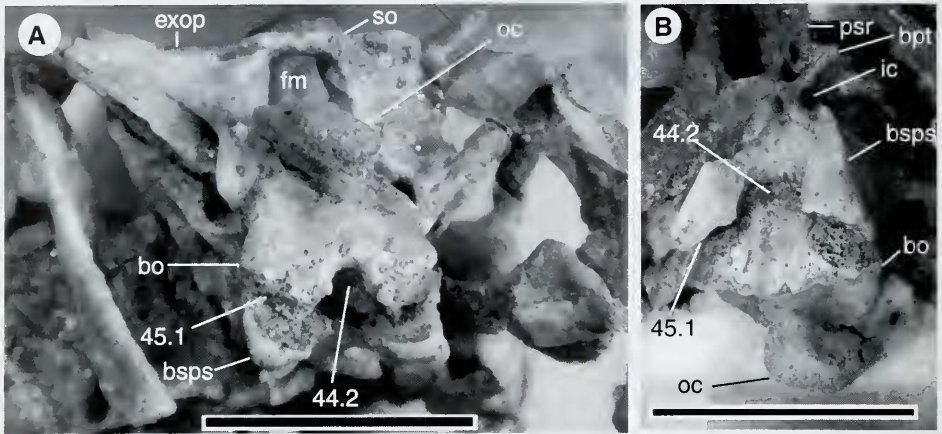


Figure 3

*Anchisaurus polyzelus*, YPM 1883. **A**, braincase in occipital view; **B**, braincase in ventral view. Numbers indicate derived character states (from Appendix 1) that are sauropod synapomorphies. Scale 20 mm.

*zelus* from Springfield, Massachusetts, represent different sized individuals of a single species. Accordingly, *Ammosaurus major* Marsh (1889) is hereby placed as a junior synonym of *Anchisaurus polyzelus* Hitchcock (1865) (NEW SYNONYMY).

Other material that has been referred to either *Anchisaurus* or *Ammosaurus* does not belong to *Anchisaurus polyzelus*. A fragmentary forelimb (YPM 2125) from the Portland Formation of East Windsor, Connecticut (Wyman 1855) was referred to *A. colurus* Marsh 1891 (a synonym of *A. polyzelus* [Galton 1976]) by Lull (1912) and Huene (1914). It can be referred to Plateosauria, within Prosauropoda, by the presence of an enlarged distal carpal 1 that overlaps distal carpal 2 (Yates 2003a; interpreted as a plateosaurian synapomorphy in this paper), a character apparently not present in *A. polyzelus* (based on YPM 1883). Two specimens from the Navajo Sandstone of Arizona (UCMP 82961 and MNA G2 7233) have been referred to

*Ammosaurus cf. major* by Galton (1976). The former also shows an enlarged distal carpal 1 that overlaps distal carpal 2 and can therefore be referred to Plateosauria. The stout proportions of the first metacarpal (proximal width exceeds its length) and the relative sizes of the manual unguals (the ungual of digit 1 is much larger than that of digit 2, which in turn is much larger than that of digit 3) indicate that this specimen is probably related to *Masospondylus carinatus* (Yates 2003a). MNA G2 7233 is an indeterminate primitive sauropodomorph that can be excluded from *Anchisaurus polyzelus* by its broad pubic apron and its large, well-developed calcaneum.

#### Revised diagnosis of *Anchisaurus polyzelus* (Hitchcock)

*Anchisaurus polyzelus* is a basal sauropod with the following autapomorphies: ventrally facing foramen for the internal

carotid artery located in a deep lateral notch of the parabasisphenoid plate (Figure 3); distance between the short basiptyergoid processes less than the width of the basal tubera (Galton 1985; Figure 3); lateral pit on the distal quadrate, just above the articular condyle (Figure 4); large surangular foramen (dorsoventral diameter about 30% of the dorsoventral height of the surangular) below the apex of the coronoid process (Figure 5); foramen opening ventrally at the base of the second sacral rib (first primordial sacral [Figure 1]); large fenestra piercing the third sacral rib (second primordial sacral [Figure 1]); long, narrow preacetabular blade of the ilium at least twice as long as high at its base; ventrally emarginate obturator plate of the ischium; flat, coplanar ischial blades (Figure 2) and an obturator foramen that occupies most of the obturator plate of the pubis.

### Sauropod-like Features of *Anchisaurus polyzelus*

Before a discussion of the character data can begin it is necessary to discuss the underlying phylogenetic assumptions used to determine character polarities in this study. It is assumed that *Marasuchus lilloensis*, *Pseudolagosuchus major*, Ornithischia, Herrerasauridae and Theropoda (consisting of Coelophysoidea, Ceratosauria and Tetanurae) form serially closer outgroups to Sauropodomorpha (in the broad stem-based sense). The placement of Herrerasauridae (based largely on *Herrerasaurus ischigualastensis*) outside of Theropoda follows recent arguments by Fraser and others (2002) and the phylogenetic analyses of Langer (2001, in press)

and Yates (2003a). This systematic arrangement is far from universally accepted and there can be little doubt that *Herrerasaurus ischigualastensis* presents a difficult systematic problem. Its anatomy displays two sets of morphological data that support different systematic positions. On the one hand there is a suite of derived characters that it shares with theropods to the exclusion of other dinosaurs (Serenó and others 1993), whereas on the other hand it retains several plesiomorphic features that suggest it lies outside the clade uniting Theropoda with Sauropodomorpha. These plesiomorphic features include: a large caudolateral process of the premaxilla that forms a long suture with the nasal, behind the external naris; a subnarial foramen that is no larger than the maxillary nutritive foramina and lies outside of the narial fossa (in contrast to large subnarial foramen on the margin of, or within, the narial fossa) (Fraser and others 2002); a block-shaped lacrimal (in contrast to inverted L-shape) (Rauhut 2000); short posterior cervical vertebrae (vertebrae 7 to 9) that are no longer than the axis (Yates 2003a); distal carpal 1 is smaller than distal carpal 2; the third finger is the longest digit of the manus (Padian 1997). Clearly, one set of data is giving a misleading signal. The first set may be a suite of convergences or the second set may be a suite of reversals. When both sets of data are combined in a cladistic analysis a nontheropod position of *Herrerasaurus ischigualastensis* is supported in the most parsimonious trees (Langer 2001, in press; Yates 2003a) but a Templeton test reveals that this support is not significant (Langer, in press). However, if the characters that unite *Herrerasaurus*

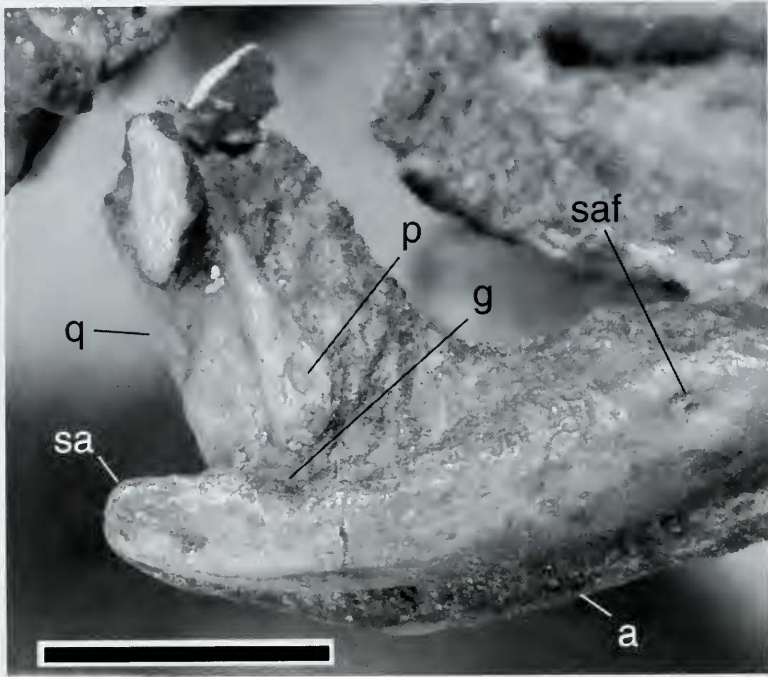


Figure 4

*Anchisaurus polyzelus*, YPM 1883, right jaw joint in lateral view. Scale 10 mm.

*ischigualastensis* with Theropoda are examined, it can be seen that they are functionally linked to hypercarnivory. For instance, an intermandibular joint allows the jaws to clamp around struggling prey (Sereno and Novas 1993), elongate penultimate phalanges and trenchant unguis are clear adaptations for grasping prey and the elongate distal caudal prezygapophyses would stiffen the distal tail and allow it to act as a dynamic stabilizer during struggles with prey. Although functional relationship is a poor reason for rejecting a suite of character data a priori (Gauthier 1986), it does help us decide which of two conflicting suites of character data is more likely to be spurious. In this case it seems that

convergence between *Herrerasaurus ischigualastensis* and Theropoda due to a similar lifestyle is a better explanation of the data than the ad hoc assumption that *Herrerasaurus ischigualastensis* underwent a suite of apparently capricious reversals. Thus, the position of *Herrerasaurus ischigualastensis* outside of Theropoda + Sauropodomorpha is the preferred hypothesis in this paper.

#### *Tooth enamel with a wrinkled surface*

(Wilson and Sereno 1998; Wilson 2002)

The wrinkled texture of the tooth enamel of *A. polyzelus* has not been recognized in the past, probably because most of the exposed enamel lost its surface during prepa-



ration. However, small patches of undamaged enamel can be seen near the bases of the first two teeth in the right dentary (Figure 6b). The enamel is sculpted with short longitudinal wrinkles that are similar to, though smaller than, those seen on sauropod teeth (Wilson and Sereno 1998). In contrast, other sauropodomorph and theropod teeth (except those of spinosaurids) are smooth (Figure 6a).

#### *Procumbent maxillary and dentary teeth* (Gauthier 1986; Upchurch 1998)

The long axes of the teeth of ornithischians, basal saurischians, nearly all theropods, and prosauropods stand at right angles to the margins of the tooth-bearing bones. In contrast, most of the maxillary (the first two may be erect) and posterior dentary teeth of most sauropods lean forward (for example, in *Shunosaurus lii*, 45° to 50° [Zhang 1988, fig. 21]; in *Omeisaurus tianfuensis*, 45° to 72° [He and others 1988, fig. 15a]; in *Diplodocus longus*, 35° to 80° [Ostrom and McIntosh 1966, pl. 1]; in *Camarasaurus lentus*, 70° to 80° [Madsen and others 1995, fig. 5]). The maxillary teeth of *Anchisaurus polyzelus* are also distinctly procumbent (51° to 72° [Figure 5]). Unfortunately, complete dentary teeth are restricted to the rostral end of the jaws, where they are erect, so it is not possible to determine if the more caudal dentary teeth had a similar lean as the maxillary teeth.

The prosauropods *Lufengosaurus huenei* and *Massospondylus carinatus* display distinctly procumbent dentary teeth (Young 1951; personal observation of SAM K1314), but unlike *Anchisaurus polyzelus* and sauropods, the maxillary teeth remain erect. Other specimens referred to

*M. carinatus* (for example, BP/1/4934 [Gow and others 1990, fig. 9]) have erect teeth in both the upper and lower jaws. Only one supposed prosauropod, *Mus-saurus patagonicus*, has procumbent teeth in both the upper and lower jaws (Bonaparte and Vince 1979). However, there are characteristics of this taxon (such as an expanded rostral end of the dentary, exclusion of the frontal from the supratemporal fossa, ischia that exceed the pubes in length, and flattened blade-like distal ischia; personal observation of PVL 4068 and 4210) that cast doubt on its identification as a prosauropod.

#### *Loss of the antorbital fossa from the rostroventral corner of the lacrimal* (Modified from Upchurch 1998; Wilson and Sereno 1998; Wilson 2002)

The antorbital fossa of most saurischians extends over a triangular flange projecting from the rostroventral corner of the lacrimal (*Herrerasaurus ischigualastensis* [Sereno and Novas 1993, fig. 1]; *Eoraptor lunensis* [Sereno and others 1993, fig. 1]; *Allosaurus fragilis* [Gilmore 1920, fig. 8]; *Saturnalia tupiniquim* [personal observation of MCP 3845-PV]; *Thecodontosaurus caducus* [Yates 2003a]; *Plateosaurus engelhardti* [Galton 1984a, fig. 3a]). In most sauropods the antorbital fossa is absent or is restricted to the dorsal end of the ascending ramus of the maxilla (*Jobaria tiguidensis* [Sereno and others 1999, fig. 2a]). The near total loss of the antorbital fossa has been used as a diagnostic character of Eusauropoda in several phylogenetic analyses of sauropod interrelationships (Upchurch 1998; Wilson and Sereno 1998; Wilson 2002). Correlated with this is the transformation of the ventral ramus



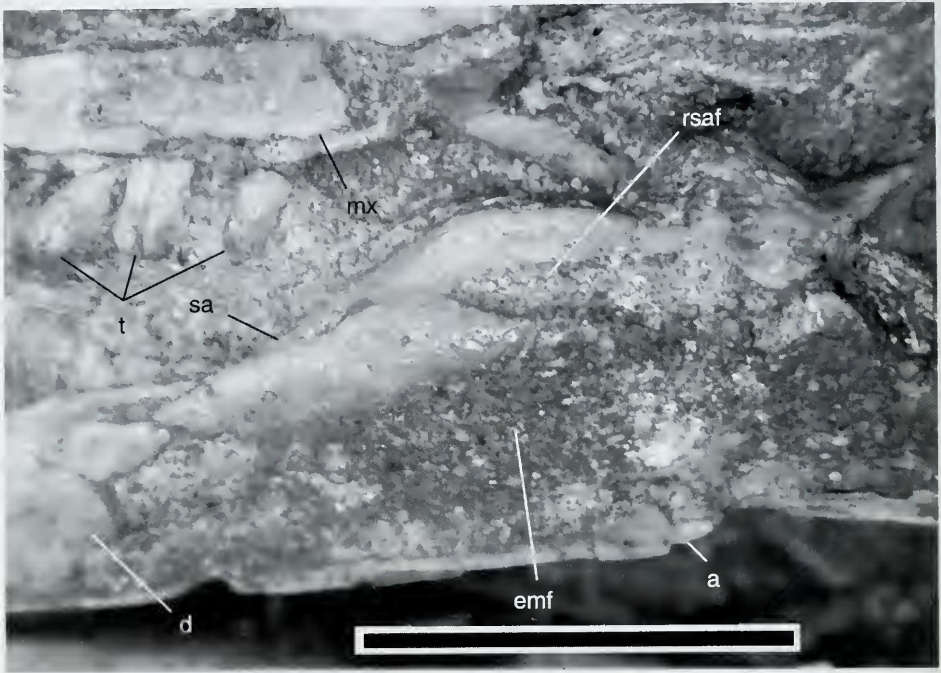


Figure 5

*Anchisaurus polyzelus*, YPM 1883, left coronoid region of the lower jaw in lateral view. Scale 20 mm.

of the lacrimal to a simple pillar that lacks the rostroventral flange. *Anchisaurus polyzelus* maintains a well-developed antorbital fossa on the maxilla, but it does not extend onto the rostroventral corner of the lacrimal. Furthermore, the ventral end of the lacrimal is pillar-like and lacks a rostrally projecting triangular flange (Figure 7). Thus the loss of the antorbital fossa can be seen as at least a two-stage affair, beginning on the lacrimal in the caudoventral corner of the antorbital fenestra and extending forward on the maxilla.

*Transversely expanded ventral ramus of the postorbital* (Wilson and Sereno 1998; Wilson 2002)  
The mediolateral width of the ventral

ramus of the postorbital does not exceed its rostrocaudal width in most theropods (*Ceratosaurus magnicornis* [Madsen and Welles 2000, pl. 5a, b]) and nonsauropod sauropodomorphs (*Thecodontosaurus antiquus* [personal observation of BRSUG 26660]). In *Anchisaurus polyzelus* and most sauropods, the ventral ramus of the postorbital is transversely expanded so that the mediolateral width exceeds the rostrocaudal width at its midlength (Figure 8). In *A. polyzelus* the ratio of mediolateral width to the rostrocaudal width is 1.76, whereas in other sauropods it ranges from 1.43 (*Camarasaurus grandis* [Madsen and others 1995]) to 2.0 (*Apatosaurus excelsus* [measured from a cast of TATE 099]). Some theropods (for example,

*Afrovenator abakensis* [Sereno and others 1993], and *Torvosaurus tanneri* [Britt 1991]) have a ventral ramus that is transversely expanded, but unlike the condition in Sauropoda the caudal side of the ramus is deeply concave. Furthermore, the distribution of the character within Theropoda is such that it clearly does not represent the plesiomorphic condition for that clade.

The primitive condition is present in the basal eusauropod *Shunosaurus lii* (Wilson and Sereno 1998), thus there could have been a reversal of the derived condition, or it may have been convergently acquired in *Anchisaurus polyzelus* and more derived sauropods.

*Lower temporal fenestra extends under the orbit for more than 25% of its length* (Upchurch 1995, 1998; Wilson and Sereno 1998; Wilson 2002)

The lower temporal fenestra of *Herrerasaurus ischigualastensis*, *Eoraptor lunensis*, theropods and prosauropods is positioned almost entirely behind the orbit. If any overlap does occur, it is minimal and occupies no more than 15% of the length of the orbit. In contrast, the lower temporal fenestra of eusauropods (such as *Camarasaurus lentus* [Madsen and others 1995, fig. 5]) and *Anchisaurus polyzelus* does extend underneath the orbit for at least a quarter of its length. The marked brevity of the infraorbital bar of the jugal in YPM 1883 indicates that the condition is real, rather than the result of postmortem crushing.

*Exclusion of the frontal from the supratemporal fossa*

(Gauthier 1986; Upchurch 1998; Wilson

and Sereno 1998; Wilson 2002)

The supratemporal fossa extends onto the frontal in basal ornithischians, basal saurischians, theropods, basal sauropodomorphs and prosauropods. In *A. polyzelus*, *Omeisaurus tianfuensis* (Wilson and Sereno 1998), *Jobaria tiguidensis* (Sereno and others 1999) and Neosauropoda (*Camarasaurus lentus* [Madsen and others 1995, fig. 6a]) the postorbital and the parietal contact broadly to exclude the frontal from the upper temporal fossa. As in the case of the transverse expansion of the ventral ramus of the postorbital, this character is rendered ambiguous by the presence of the primitive condition in *Shunosaurus lii* (Wilson and Sereno 1998).

*Quadrato foramen is absent*

The basal condition for Saurischia is to have the quadrato foramen deeply incised into, and partly encircled by, the body of the quadrato. This incision occurs no higher than halfway up the quadrato and is bounded laterally by the ascending ramus of the quadratojugal. This condition is seen in *Herrerasaurus ischigualastensis* (Sereno and Novas 1993, fig. 1g), many theropods (such as *Dilophosaurus wetherilli* [Welles 1984, fig. 5]; *Allosaurus fragilis* [Madsen 1976, pl. 3e]), basal sauropodomorphs (*Saturnalia tupiniquim* [personal observation of MCP 3845-PV]; *Thecodontosaurus antiquus* [personal observation of BRSUG 26596]; *Efraasia minor* [Galton and Bakker 1985, fig. 3b]) and prosauropods (*Plateosaurus engelhardti* [personal observation of GPIT skelett 1]). In contrast, the quadrato foramen is absent in eusauropods, in which the dorsal ramus of the quadratojugal

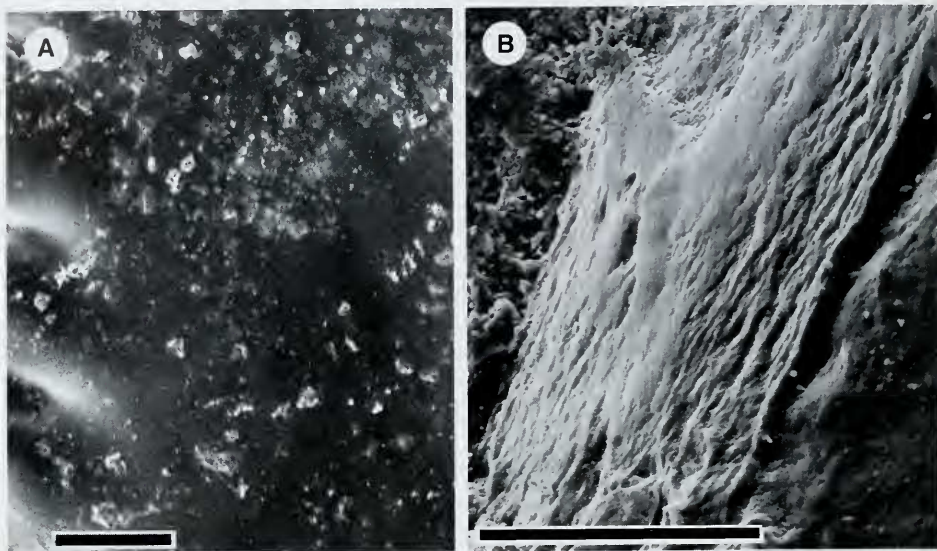


Figure 6

Scanning electron micrographs of the surface texture of the tooth enamel. **A**, *Thecodontosaurus antiquus*, BRSUG 26651; **B**, *Anchisaurus polyzelus*, YPM 1883. Images obtained by casting silicone rubber peels of the original specimens in epoxy resin for microscopy. Scale 0.5 mm.

contacts the lateral margin of the quadrate along its entire length (*Camarasaurus lentus* [Madsen and others 1995, fig. 20]). The left quadrate of YPM 1883 shows that the lateral margin of the quadrate that would have contacted the quadratojugal was entire and has no trace of any incision, so we can be sure that the quadrate foramen was absent.

The polarity of this character is not dependent on the placement of *Herrerasaurus ischigualstensis* basal to the theropod–sauropodomorph clade, so long as *Saturnalia tupiniquim* and *Thecodontosaurus antiquus* remain as basal outgroups to all other sauropodomorphs. The latter systematic placements are robust hypotheses (Langer 2001; Yates 2003a; the present analysis), so I am confident the polarity has been correctly interpreted.

*Ventral margin of the braincase V-shaped with lowered basal tubera and a raised parasphenoid rostrum*

The primitive dinosaur braincase has a straight ventral margin, and the occipital condyle, basal tuber, basiptyergoid process and parasphenoid rostrum are arranged linearly in horizontal view (Figure 9a). This shape can be seen in basal sauropodomorphs such as *Saturnalia tupiniquim* (personal observation of MCP 3845-PV) and *Thecodontosaurus antiquus* (Benton and others 2000, fig. 6b). Prosauropods and sauropods both have modified braincase shapes, but these differ. In prosauropods the basiptyergoid ventral margin is depressed so that the parasphenoid rostrum and the basiptyergoid process lie below the level of the basal tuber, which in turn lies below the lower edge of the oc-

cipital condyle (Figure 9b). In effect the ventral margin is L-shaped, with a descending caudal portion behind the basiptyergoid processes and a horizontal section in front of them. In eusauropods the foreshortened braincase has a bent ventral margin with the basal tuber placed well below the level of the occipital condyle, while the parasphenoid rostrum is raised up so that its tip lies above the level of the ventral rim of the occipital condyle (Figure 9c). The base of the basiptyergoid process is also raised so that it lies somewhere between the level of the basal tuber and the ventral margin of the parasphenoid rostrum, although the distal tip of this process usually protrudes below the basal tuber. In effect the ventral margin is V-shaped with a descending section behind the basal tubera and a steeply ascending section in front of them. The braincase of YPM 1883 is not foreshortened as it is in other sauropods, but is bent in the same way (Figure 9d). The basal tuber is depressed well below the level of the occipital condyle while the braincase floor rostral to it slopes upward toward the parasphenoid rostrum. Although the basal part of the parasphenoid rostrum has been lost because of damage sustained during collection or early preparation, the tip of the rostrum is held firmly in place by its surrounding matrix. A lateral view shows that its dorsal margin lies entirely above the occipital condyle (Figure 9d).

*Deep U-shaped fossa opening caudally between the basal tubera*

The basal tubera of primitive dinosaurs such as *Lesothosaurus diagnosticus* (Sereno 1991, fig. 11 c, d) and *Herrerasaurus ischi-*

*gualastensis* (Sereno and Novas 1993, fig. 7c, e) are rugose knobs that project from the lateral ends of a raised transverse bar that is developed on, or about, the basioccipital–basisphenoid suture. The bar sometimes has a small central notch, as in *H. ischigualastensis*. In contrast, there is no transverse bar in *Anchisaurus polyzelus* (Figure 3) and eusauropods (such as *Shimosaurus lii* [Zhang 1988, figs. 11, 13]; *Apatosaurus ajax* [Berman and McIntosh 1978, fig. 11b]; *Camarasaurus grandis* [Madsen and others 1995, fig. 33c]). Their basal tubera are widely separated by a deep fossa. In ventral view, this fossa is a caudally opening, U-shaped depression impressed into the parasphenoid–basisphenoid plate (Figure 3).

*Transverse notch bounded by unfinished, spongy bone between the basioccipital and basisphenoid components of each basal tuber*

The basal tubera of theropods, basal sauropodomorphs and prosauropods are fully ossified and are covered with dense compact bone up to their tips. The basal tubera of *Anchisaurus polyzelus* and sauropods (such as *Camarasaurus grandis* [Madsen and others 1995, fig. 33c] and *Apatosaurus ajax* [Berman and McIntosh 1978, fig. 11b]) are distinctly different. In these taxa a transverse notch crosses the tip of each basal tuber; the basioccipital forms a ventrally facing wall of the notch and the basisphenoid forming the caudally facing walls (Figure 3). The notch was almost certainly filled with a cartilaginous extension of the basal tuber because both of these walls are formed by unfinished spongy bone (Figure 3). The character is not age related because an immature spec-



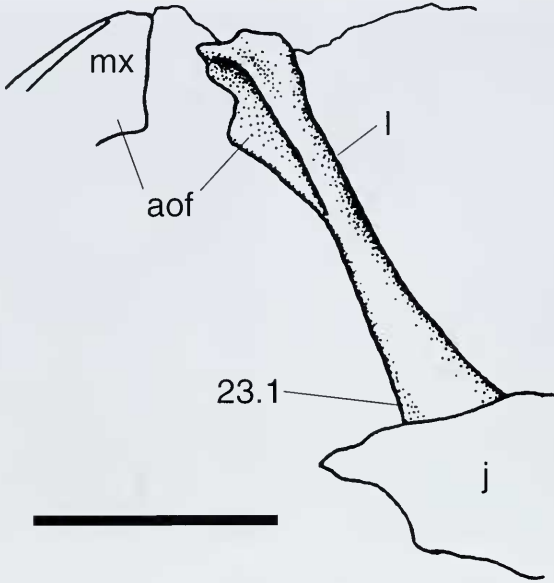


Figure 7

*Anchisaurus polyzelus*, YPM 1883, left lacrimal region of the skull in lateral view. Numbers indicate derived character states (from Appendix 1) that are sauropod synapomorphies. Scale 10 mm.

imen of the basal sauropodomorph *Thecodontosaurus caducus* (Kermack 1984, fig. 8) fails to show the derived condition, while adult sauropods still lack fully ossified basal tubera.

*Loss of a well-defined fossa on the distal flexor surface of the humerus*

Primitively, archosaurs have a well-defined fossa on the cranial surface of the distal humerus, between the radial and ulnar condyles. This fossa is semicircular and has a sharply defined proximal border. It is retained in basal ornithischians (personal observation of *Scelidosaurus harrisonii*, BRSMG Ce12785ch), theropods (such as *Megapnosaurus rhodesiensis* [Raath 1990, fig. 7.4]), basal sauropodomorphs (personal observation of *Thecodontosaurus antiquus*, BRSUG 23610) and

prosauropods (such as *Plateosaurus engelhardti* [Galton 1990, fig. 15.6c]). In *Anchisaurus polyzelus* (Figure 10) and other sauropods (for example, *Camarasaurus grandis* [Ostrom and McIntosh 1966, pl. 49]), the distal flexor surface is flat to gently concave and lacks a semicircular fossa. This character may be associated with graviportalism because the fossa is independently lost in graviportal stegosaurs (*Stegosaurus ungulatus* [Ostrom and McIntosh 1966, pl. 33]).

*Manus shortened relative to the rest of the forelimb so that it is less than 40% of the humerus + radius*  
(Polarity reversed from Sereno and others 1993)

Sereno and others (1993) noted that the hands of *Herrerasaurus ischigualastensis*



Table 1

The terminal taxa used in the cladistic analysis and the literature used in coding in the character data. Taxa marked with an asterisk were coded from specimens with supplementary data from the literature; those without an asterisk were coded entirely from the literature.

| OTU                                      | Literature   |
|--|--|
| Ornithischia*                            | Thulborn 1972; Santa Luca 1980; Sereno 1991                        |
| <i>Herrerasaurus ischigualastensis</i> * | Novas 1993; Sereno 1993; Sereno and Novas 1993                     |
| Theropoda*                               | Gilmore 1920; Madsen 1976; Welles 1984;<br>Currie and Zhao 1993    |
| <i>Saturnalia tupiniquim</i> *           | Langer and others 1999   |
| <i>Thecodontosaurus</i> spp.*            | Benton and others 2000   |
| <i>Anchisaurus polyzelus</i> *           | Galton 1976  |
| <i>Riojasaurus incertus</i> *            | Bonaparte 1972; Bonaparte and Pumares 1995                         |
| <i>Efraasia minor</i> *                  | Galton 1973, 1984b, 1985a; Galton and Bakker 1985                  |
| <i>Plateosaurus engelhardti</i> *        | Huene 1926; Galton 1984a, 1985b                                    |
| <i>Massospondylus carinatus</i> *        | Hoepen 1920a, 1920b; Cooper 1981; Gow 1990;<br>Gow and others 1990 |
| <i>Lufengosaurus huenei</i>              | Young 1941a, 1941b   |
| <i>Coloradisaurus brevis</i> *           | Bonaparte 1978   |
| <i>Melanorosaurus readi</i> *            | Heerden and Galton 1997  |
| <i>Blikanasaurus cromptoni</i>           | Galton and Heerden 1998  |
| <i>Kotasaurus ymanpalliensis</i>         | Yadagiri 2001  |
| <i>Vulcanodon karibaensis</i>            | Raath 1972; Cooper 1984  |
| <i>Shunosaurus lii</i>                   | Zhang 1988   |
| <i>Barapasaurus tagorei</i>              | Jain and others 1979; Wilson and Sereno 1998                       |
| <i>Omeisaurus tianfuensis</i>            | He and others 1988   |
| Neosauropoda*                            | Janensch 1935–1936; Gilmore 1936;<br>Madsen and others 1995        |

and theropods are considerably elongated (more than 45% of the length of the humerus + radius) and used the character as evidence that the former species belongs to the latter clade. However, the condition is interpreted here as diagnostic of the Saurischia as a whole, regardless of the systematic position of *Herrerasaurus*, because such elongated hands are also present in the basal sauropodomorphs *Thecodontosaurus antiquus* (personal

observation of YPM 2195) and *Efraasia minor* (Galton 1973). Prosauropods have shorter hands that range between 40% and 45% of the humerus + radius (such as *Plateosaurus engelhardti* [Huene 1926]). In *Anchisaurus polyzelus* and most Sauropoda, the hands are shorter still: the manus is 38% of the humerus + radius in YPM 1883, whereas it is 29% in *Shunosaurus lii* (Zhang 1988), 20% in *Omeisaurus tianfuensis* (He and others

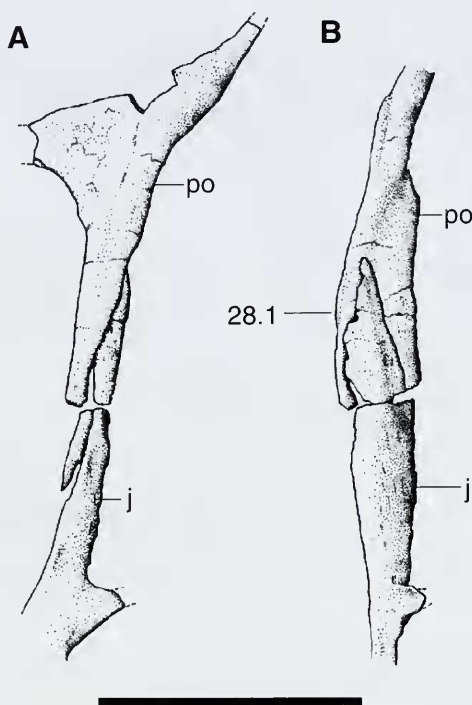


Figure 8

*Anchisaurus polyzelus*, YPM 1883, left postorbital bar. **A**, lateral view; **B**, caudal view. Numbers indicate derived character states (from Appendix 1) that are sauropod synapomorphies. Scale 10 mm.

1988) and 33% in *Apatosaurus louisae* (Gilmore 1936).

*Pubic apron narrowed relative to the pubic basin*

In basal dinosauiromorphs (such as *Lagerpeton chanarensis* [Sereno and Arcucci 1993, fig. 1b]), the conjoined pubes are rather straight-sided in cranial view. The width of the pubic apron is more than half the width of the pubic basin (measured by the distance between the iliac peduncles). Basal saurischians (for example, *Herrerasaurus ischigualastensis* [Novas 1993, fig. 6]) and prosauropods

(*Plateosaurus engelhardti* [Huene 1926, fig. 3]) have retained this condition. In contrast, *Anchisaurus polyzelus* (YPM 208, 1883; Figure 11) and sauropods (*Vulcanodon karibaensis* [Cooper 1984, fig. 17]; *Camarasaurus grandis* [Ostrom and McIntosh 1966, pl. 89]) have a pubic apron that is, at midlength, no more than 40% of the distance between the iliac peduncles. The derived condition is convergently developed in many theropods.

*Flattened ischial blades*

(Wilson and Sereno 1998; Wilson 2002) This character has a complex distribution

Table 2

The terminal taxa that were examined firsthand and the specimen numbers of the specimens examined; (c) indicates that only a cast of the specimen was examined.

|  |   |
|--|---|
| Ornithischia                           | BMNH R111, RU.B17, RU.B23, SAM K1332  |
| <i>Herrerasaurus ischigualastensis</i> | PVL 2566  |
| Theropoda                              | BMNH RU.P76/1, HMN MB.R.2175.7.4, UCMP 47721(c), HMN unnumbered (holotype of <i>Elaphrosaurus bambergi</i> ), MOR 693 (c) |
| <i>Saturnalia tupiniquim</i>           | MCP 3844-PV, 3845-PV  |
| <i>Thecodontosaurus</i> spp.           | BMNH RU.P24, RU.P24/3, RU.P77/1, YPM 2192, 2195, many BRSUG and BRSMG specimens   |
| <i>Anchisaurus polyzelus</i>           | YPM 208, 209, 1883, AM 41/109(c)  |
| <i>Riojasaurus incertus</i>            | PVL 3526, 3662, 3663, 3805, 3808, PULR 56   |
| <i>Efraasia minor</i>                  | SMNS 12354, 12667, 12668, 12684, 12843, 14881   |
| <i>Plateosaurus engelhardti</i>        | GPIT skelett 1, skelett 2, SMNS 12950, 13200, HMN MB.R.1937, skelett 25   |
| <i>Massospondylus carinatus</i>        | BPI 4376, 4693, 4779, 4930, 4934, 4955, 5238, 5241, SAM 1314(c)   |
| <i>Coloradisaurus brevis</i>           | PULR unnumbered, PVL 3967, unnumbered (field no. 6)   |
| <i>Melanorosaurus readi</i>            | NM R1551  |
| Neosauropoda                           | HMN MB.R2181, MB.R2223.2.2, MB.R222.2.3, MB.R2249 TATE 099(c), YPM 1980, 1225   |

that by itself does not provide particularly compelling evidence for a close relationship between *Anchisaurus polyzelus* and sauropods. The ischia of basal dinosauro-morphs have flattened, blade-like shafts in which the transverse width greatly exceeds the dorsoventral depth. In contrast, the ischial shafts of basal saurischians (such as *Herrerasaurus ischigualastensis* [Novas 1993] and *Guaibasaurus candelariensis* [Bonaparte and others 1999]) and theropods are rod-like, with the dorsoventral depth subequal to, or even exceeding, the transverse width. Thus, rod-like ischia seem to be the primitive condition for Sauropodomorpha sensu lato, and this condition is retained in *Thecodontosaurus*

*caducus* (Yates 2003a), *Efraasia minor* (personal observation of SMNS 12354) and Prosauropoda (for example, *Massospondylus carinatus* [Cooper 1981, fig. 55]). In contrast, *Anchisaurus polyzelus* (Figure 2) and sauropods have flattened ischial shafts that are much wider than they are deep. However, some basal sauropodomorphs (such as *Saturnalia tupiniquim* [personal observation of MCP 3844-PV] and *Thecodontosaurus antiquus* [personal observation of YPM 2192]) also have flattened sauropod-like ischial shafts. This casts some doubt over the primitive condition of this character at the node connecting Sauropoda and Prosauropoda (Sauropodomorpha sensu Sereno 1998).

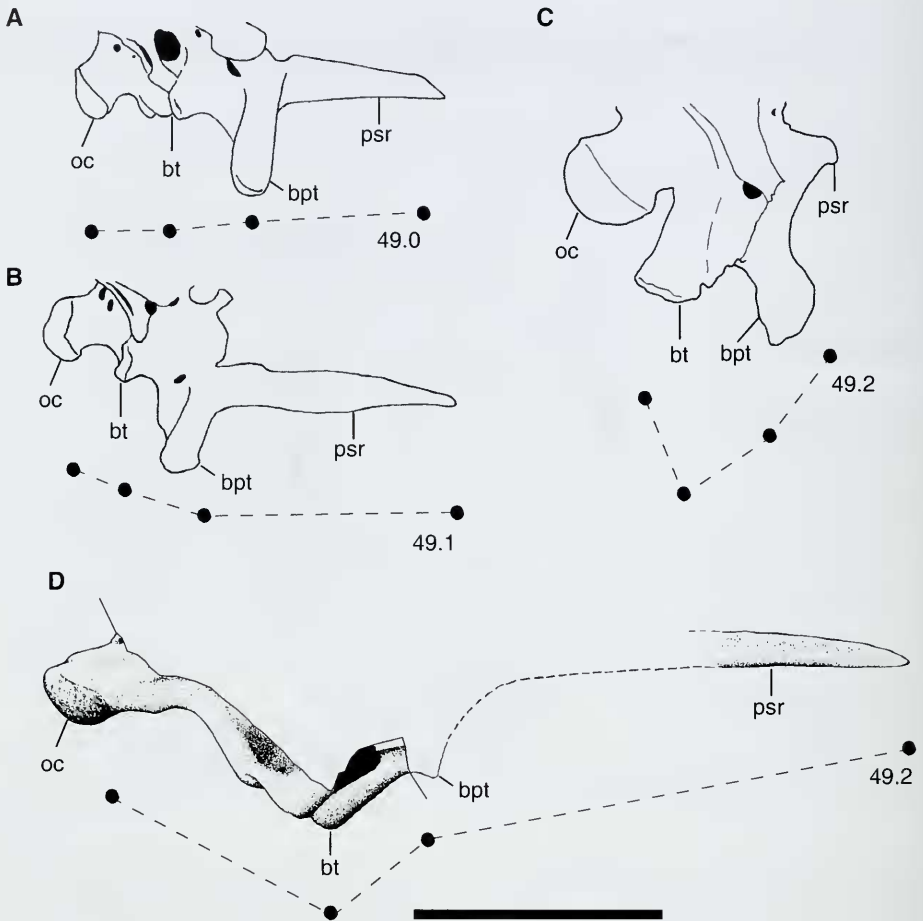


Figure 9

Sauropodomorph braincases in left lateral view. **A**, *Thecodontosaurus antiquus*, redrawn from Benton and others (2000); **B**, *Plateosaurus engelhardti*, redrawn from Galton (1984a); **C**, *Apatosaurus ajax*, redrawn from White (1958); **D**, *Auchisaurus polyzelus*, YPM 1883. Dashed lines indicate the relative positions, from left to right and marked with a spot, of the ventral edge of the occipital condyle, the peak of the basal tuber, the base of the basipterygoid process and the tip of the parasphenoid rostrum, respectively. Unshaded areas bound by solid lines in **D** represent regions that are obscured in lateral view by overlying bones. Numbers indicate the various states for character 49. **A**, **B**, **C** are not to scale; scale bar in **D** is 20 mm.

Table 3

Support measures (bootstrap frequency as a percentage and decay index) for the nodes recovered in the cladistic analysis (using *Herrerasaurus ischigualastensis* and Theropoda as outgroups). *Clade abbreviations*: mdsm, more derived sauropodomorphs; mds, more derived sauropods; mde, more derived eusauropods.

| Clade   | Bootstrap frequency % | Decay index |
|---|-----------------------|-------------|
| Sauropodomorpha                                       | 96                    | 6           |
| <i>Thecodontosaurus</i> + mdsm                        | 94                    | 4           |
| <i>Efraasia</i> + mdsm                                | 98                    | 8           |
| Prosauropoda + Sauropoda (excluding <i>Efraasia</i> ) | 57                    | —           |
| Prosauropoda (excluding <i>Efraasia</i> )             | 59                    | 3           |
| Prosauropoda (including <i>Efraasia</i> )             | 36                    | —           |
| Plateosauria  | 67                    | 3           |
| Massospondylidae                                      | 81                    | 5           |
| <i>Massospondylus</i> + <i>Lufengosaurus</i>          | 42                    | 1           |
| Sauropoda   | 97                    | 5           |
| <i>Melanorosaurus</i> + mds                           | 66                    | 1           |
| <i>Blikanasaurus</i> + mds                            | 90                    | 3           |
| <i>Kotasaurus</i> + mds                               | 88                    | 2           |
| <i>Vulcanodon</i> + Eusauropoda                       | 92                    | 3           |
| Eusauropoda   | 60                    | 1           |
| <i>Barapasaurus</i> + mde                             | 49                    | 1           |
| <i>Omeisaurus</i> + Neosauropoda                      | 78                    | 3           |

*Caudolateral process of the distal tibia fails to extend lateral to the cranio-lateral corner of the distal tibia*

(Figure 12)

The basal saurischian *Herrerasaurus ischigualastensis* has a shallow notch on the lateral side of the distal tibia that divides the descending caudolateral process from the cranio-lateral process (Novas 1993, fig. 8). When viewed distally, both processes project laterally for an equal distance (Figure 12a). In theropods, the caudolateral process extends well beyond the cranio-lateral corner of the distal tibia

(which no longer forms a discrete process, as in *Dilophosaurus wetherilli* [Welles 1984, fig. 33d]). Prosauropods also have a caudolateral process that forms the lateralmost point of the distal tibia, but in this case the projection is only slightly beyond the cranio-lateral process (*Massospondylus carinatus* [Cooper 1981, fig. 66]). The opposite condition occurs in sauropods, where the caudolateral process is much reduced and does not extend as far laterally as the cranio-lateral process (*Camarasaurus grandis* [Ostrom and McIntosh 1966, pl. 75; Figure 12e]). The



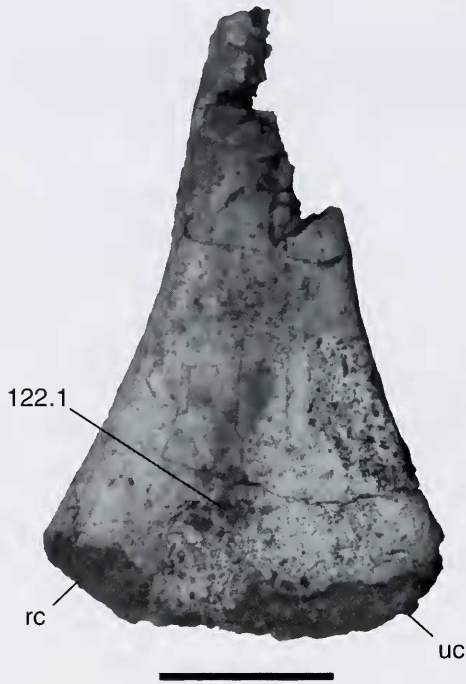


Figure 10

*Anchisaurus polyzelus*, YPM 1883, distal right humerus in cranial (flexor) view. Numbers indicate derived character states (from Appendix 1) that are sauropod synapomorphies. Scale bar 20 mm.

distal tibia of *Anchisaurus polyzelus* (YPM 208 and 1883) retains a primitive rectangular shape more like a prosauropod than the ovoid distal tibiae of derived sauropods, but does have a reduced caudolateral process that does not extend as far laterally as the cranio-lateral process does.

*Calcaneum reduced relative to the astragalus*

The mediolateral width of the calcaneum of basal sauropodomorphs and prosauropods ranges between 50% (*Saturnalia tupiniquim* [personal observation of MCP 3844-PV]) and 44% (*Coloradisaurus brevis*

[personal observation of PVL 3967]) of the width of the astragalus. The calcaneum of most sauropods is a small, globular body less than 30% of the width of the astragalus (28% in *Vulcanodon karibaensis* [Raath 1972]; *Shunosaurus lii* [Zhang 1988]; *Camarasaurus supremus* [Bonnann 2000, fig. 4]). The relatively larger calcaneum (40%) of *Diplodocus* sp. (Bonnann 2000, fig. 4) can be interpreted as a reversal (note that although it is relatively larger, it is still a simple globular body). The calcaneum of *Anchisaurus polyzelus* (YPM 1883) is reduced to the same degree as nondiplodocid sauropods (28% of the astragalus).

Table 4

Maximum femur lengths for the terminal taxa used for the square change parsimony analysis of body size evolution.

| Terminal taxon                           | Femur length<br>(mm) | Source   |
|--|----------------------|--|
| <i>Herrerasaurus ischigualastensis</i>   | 406                  | PVL 2566   |
| <i>Megapnosaurus rhodesiensis</i>        | 208                  | Raath 1990   |
| <i>Liliensternus liliensterni</i>        | 440                  | HMN MB.R.2175.7.4  |
| <i>Dilophosaurus wetherilli</i>          | 557                  | Welles 1984  |
| <i>Elaphrosaurus bambergi</i> (holotype) | 524                  | HMN unnumbered   |
| <i>Ceratosaurus magnicornis</i>          | 630                  | Madsen and Welles 2000                                       |
| <i>Siuraptor dongi</i>                   | 876                  | Currie and Zhao 1993   |
| <i>Saturnalia tupimiquim</i>             | 157                  | MCP 3845-PV  |
| <i>Thecodontosaurus antiquus</i>         | 210                  | BRSMG Ca7456   |
| <i>Efraasia minor</i>                    | 527                  | SMNS 12843   |
| <i>Riojasaurus incertus</i>              | 608                  | PVL 3808   |
| <i>Plateosaurus engelhardti</i>          | 987                  | Jain and others 1979 (as <i>Gresslyosaurus wetzelianus</i> ) |
| <i>Coloradisaurus brevis</i>             | 510                  | PVL field no. 6  |
| <i>Massospondylus carinatus</i>          | 495                  | Hoepen 1920b (as <i>Dromicosaurus gracilis</i> )             |
| <i>Lufengosaurus huenei</i>              | 555                  | Young 1941a  |
| <i>Anchisaurus polyzelus</i>             | ~275                 | Estimated from YPM 208                                       |
| <i>Melanorosaurus readi</i>              | 619                  | NM R1551   |
| <i>Blikanasaurus cromptoni</i>           | ~520                 | Estimated from data in Galton and Heerden 1998               |
| <i>Kotasaurus yamanpalliensis</i>        | 1130                 | Yadagiri 2001  |
| <i>Vulcanodon karibaensis</i>            | ~1100                | Raath 1972   |
| <i>Shunosaurus lii</i>                   | 1200                 | Wilson and Sereno 1998                                       |
| <i>Barapasaurus tagorei</i>              | 1365                 | Jain and others 1979   |
| <i>Omeisaurus tianfuensis</i>            | 1310                 | Wilson and Sereno 1998                                       |
| <i>Rayososaurus tessonei</i>             | 1440                 | Calvo and Salgado 1995                                       |
| <i>Apatosaurus excelsus</i>              | 1830                 | Wilson and Sereno 1998                                       |
| <i>Camarasaurus supremus</i>             | 1800                 | Wilson and Sereno 1998                                       |
| <i>Brachiosaurus brancai</i>             | 2140                 | Wilson and Sereno 1998                                       |

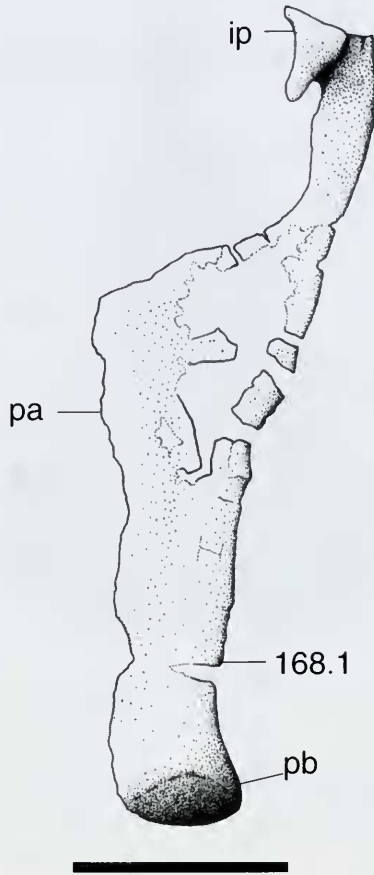


Figure 11

*Anchisaurus polyzelus*, YPM 1883, right pubis in caudal view. Numbers indicate derived character states (from Appendix 1) that are sauropod synapomorphies. Scale 50 mm.

### Cladistic Analysis

The above character data were combined with all other characters that could be found to vary among 17 ingroup taxa (for a total of 205 characters; see Appendix 1). The characters were largely culled from the literature (sources given in Appendix 1) although some novel characters were added (5, 34, 37, 44, 45, 46, 52, 63, 75, 85,

87, 88, 98, 99, 102, 116, 131, 148, 150, 166, 168, 182, 190, 191, 199). Codings were based on personal observations of most of the taxa with supplements from the literature (Tables 1 and 2).

The data matrix was analysed using PAUP v. 4.0 (Swofford 2002) using the branch-and-bound search option. All characters were weighted equally. The following characters were treated as or-

dered because they clearly formed physical transformation series: 7, 29, 43, 79, 87, 120, 132, 134, 139, 141, 171, 180, 197, 198 (to treat such characters as unordered is to ignore the similarities between state 1 and the other derived states, and thus disregard potential homologies). Super-specific taxa were coded by examination of several members from each of the basal branches of that clade, supplemented with particularly well-represented taxa.

*Rayosaurus tessonei*, *Apatosaurus* spp., *Camarasaurus* spp. and *Brachiosaurus brancai* were the main taxa used to code the Neosauropoda, while *Liliensternus liliensterni*, *Dilophosaurus wetherilli*, *Elaphrosaurus bambergi*, *Sinraptor dongi* and *Allosaurus fragilis* were the main taxa used to code the Theropoda (Tables 1 and 2). When a character was found to vary between these basal branches it was coded as polymorphic.

Two species of *Thecodontosaurus* were used to code for this terminal taxon: the type species, *T. antiquus*, and *T. caducus* (Yates 2003a). *Sellosaurus gracilis* is not used as a terminal taxon because the type seems to be a small specimen of *Plateosaurus* (Yates 2003b). Other diagnostic specimens that have been referred to *Sellosaurus gracilis* are placed in the taxon *Efraasia minor* (Yates 2003b). The binomen *Plateosaurus engelhardti* is used for the well-known and abundant taxon from Trossingen, Halberstadt, and many other localities, although it has recently been shown that the poor type specimens of *Plateosaurus engelhardti* are not conspecific with this form (Galton 2000). Nevertheless, the name has been applied to the abundant and well-known taxon for more than 100 years and it forms the

type species of several higher level taxa. It also serves as an anchor taxon in several phylogenetic definitions for important dinosaurian clades. Little can be gained by applying a new name to this taxon, and the traditional usage of the name is therefore maintained here. The coding for *Melanorosaurus readi* is based on the referred specimen (NM R1551 [Heerden and Galton 1997]), whereas the coding for *Coloradisaurus brevis* was supplemented by some undescribed specimens (unregistered PVL specimen, field no. 6, and an unregistered PULR specimen) that share autapomorphies with the holotype (Yates, unpublished data).

The choice of outgroup is important because it does exert an affect on character polarities and the interpretation of character evolution at the base of the tree. As outlined above, Theropoda and *Herrerasaurus ischigualastensis* are the preferred outgroups and both the tree description (Appendix 3) and the analysis of the evolution of body size both use them. Nevertheless, an alternative analysis was run using Ornithischia (codings based largely on *Lesothosaurus diagnosticus*, *Scelidosaurus harrisonii* and *Heterodontosaurus tucki*) and an expanded Theropoda (combined codings for Theropoda and *Herrerasaurus ischigualastensis*) as outgroups. This was done to determine the sensitivity of the internal topology to outgroup choice. In all cases the robustness of each of the nodes was tested by determining decay indices and bootstrap frequencies. Decay indices were determined by multiple searches for suboptimal trees (increasing tree length by one step for each search) and recording which clades collapse in the strict consensus of each

Table 5

Results of the square change parsimony analysis of femur length in sauropodomorph evolution for both most-parsimonious trees. For each taxon the reconstructed ancestral length (not applicable to terminal taxa) and the amount of change on the branch that supports it are given. Asterisks indicate those changes that exceed one standard deviation from the mean magnitude of change (regardless of sign). *Clade abbreviations*: mds, more derived sauropodomorphs; mds, more derived sauropods; mde, more derived eusauropods.

| Tree A                      |                       |             | Tree B                      |                       |             |
|-----------------------------|-----------------------|-------------|-----------------------------|-----------------------|-------------|
| Taxon                       | Ancestral length (mm) | Change (mm) | Taxon                       | Ancestral length (mm) | Change (mm) |
| Saurischia                  | 441.4                 | —           | Saurischia                  | 440.1                 | —           |
| <i>Herrerasaurus</i>        | —                     | 18.6        | <i>Herrerasaurus</i>        | —                     | 19.9        |
| Theropoda                   |                       |             | Theropoda                   |                       |             |
| + Sauropodomorpha           | 422.8                 | -18.6       | + Sauropodomorpha           | 420.3                 | -19.9       |
| Theropoda                   | 526.9                 | 104.0       | Theropoda                   | 525.8                 | 105.5       |
| Sauropodomorpha             | 300.2                 | -122.6      | Sauropodomorpha             | 294.9                 | -125.3      |
| <i>Saturnalia</i>           | —                     | -143.2      | <i>Saturnalia</i>           | —                     | -137.9      |
| <i>Thecodontosaurus</i>     |                       |             | <i>Thecodontosaurus</i>     |                       |             |
| + mds                       | 320.9                 | 20.6        | + mds                       | 307.5                 | 12.6        |
| <i>Thecodontosaurus</i>     | —                     | -110.9      | <i>Thecodontosaurus</i>     | —                     | -97.5       |
| <i>Efraasia</i> + mds       | 452.4                 | 131.5       | Prosauropoda                |                       |             |
| <i>Efraasia</i>             | —                     | 74.6        | + Sauropoda                 | 417.7                 | 110.2       |
| Prosauropoda                |                       |             | Prosauropoda                | 522.2                 | 104.5       |
| + Sauropoda                 | 509.2                 | 56.9        | <i>Efraasia</i>             | —                     | 4.8         |
| Prosauropoda                | 617.1                 | 107.8       | <i>Riojasaurus</i>          |                       |             |
| <i>Riojasaurus</i>          | —                     | -9.1        | + Plateosauria              | 622.0                 | 99.8        |
| Plateosauria                | 733.9                 | 116.9       | <i>Riojasaurus</i>          | —                     | -14.0       |
| <i>Plateosaurus</i>         | —                     | 253.1*      | Plateosauria                | 735.8                 | 113.8       |
| Massospondylidae            | 597.7                 | -136.2      | <i>Plateosaurus</i>         | —                     | 251.2*      |
| <i>Coloradisaurus</i>       | —                     | -87.7       | Massospondylidae            | 598.4                 | -137.4      |
| <i>Massospondylus</i>       |                       |             | <i>Coloradisaurus</i>       | —                     | -88.4       |
| + <i>Lufengosaurus</i>      | 549.2                 | -48.5       | <i>Massospondylus</i>       |                       |             |
| <i>Massospondylus</i>       | —                     | -54.241     | + <i>Lufengosaurus</i>      | 549.5                 | -49.0       |
| <i>Lufengosaurus</i>        | —                     | 5.8         | <i>Massospondylus</i>       | —                     | -54.5       |
| Sauropoda                   | 458.3                 | -51.0       | <i>Lufengosaurus</i>        | —                     | 5.5         |
| <i>Anchisaurus</i>          | —                     | -183.3*     | Sauropoda                   | 423.3                 | 5.6         |
| <i>Melanorosaurus</i> + mds | 590.6                 | 132.3       | <i>Anchisaurus</i>          | —                     | -148.3      |
| <i>Melanorosaurus</i>       | —                     | 28.4        | <i>Melanorosaurus</i> + mds | 577.2                 | 153.9       |
| <i>Blikanasaurus</i> + mds  | 694.5                 | 103.9       | <i>Melanorosaurus</i>       | —                     | 41.8        |
| <i>Blikanasaurus</i>        | —                     | -174.5*     | <i>Blikanasaurus</i> + mds  | 689.4                 | 112.2       |

Continued.



Table 5 continued

| Tree A                    |                       |             | Tree B                    |                       |             |
|---------------------------|-----------------------|-------------|---------------------------|-----------------------|-------------|
| Taxon                     | Ancestral length (mm) | Change (mm) | Taxon                     | Ancestral length (mm) | Change (mm) |
| <i>Kotasaurus</i> + mds   | 972.9                 | 278.4*      | <i>Blikanasaurus</i>      | —                     | -169.4*     |
| <i>Kotasaurus</i>         | —                     | 157.1       | <i>Kotasaurus</i> + mds   | 970.9                 | 281.5*      |
| <i>Vulcanodon</i>         |                       |             | <i>Kotasaurus</i>         | —                     | 159.1       |
| + Eusauropoda             | 1094                  | 121.1       | <i>Vulcanodon</i>         |                       |             |
| <i>Vulcanodon</i>         | —                     | 6.0         | + Eusauropoda             | 1093                  | 122.1       |
| Eusauropoda               | 1210                  | 116.0       | <i>Vulcanodon</i>         | —                     | 7.0         |
| <i>Shunosaurus</i>        | —                     | -10.0       | Eusauropoda               | 1209                  | 116.0       |
| <i>Barapasaurus</i> + mde | 1335                  | 125.0       | <i>Shunosaurus</i>        | —                     | -9.0        |
| <i>Barapasaurus</i>       | —                     | 30.0        | <i>Barapasaurus</i> + mde | 1334                  | 125.0       |
| <i>Omeisaurus</i>         |                       |             | <i>Barapasaurus</i>       | —                     | 31.0        |
| + Neosauropoda            | 1429                  | 94.0        | <i>Omeisaurus</i>         |                       |             |
| <i>Omeisaurus</i>         | —                     | -119.0      | + Neosauropoda            | 1429                  | 95.0        |
| Neosauropoda              | 1642                  | 213.0*      | <i>Omeisaurus</i>         | —                     | -119.0      |
|                           |                       |             | Neosauropoda              | 1642                  | 213.0*      |

search. The bootstraps were run with the branch-and-bound search option and 1000 replicates.

Analysis of the matrix (Appendix 2) using *Herrerasaurus ischigualastensis* and Theropoda as outgroups produced two most-parsimonious trees (tree length 412, consistency index of 0.553, retention index of 0.724). The trees differ only in the placement of *Efraasia minor*, which is either the sister group to all other prosauropods or the sister group to Prosauropoda + Sauropoda. The supporting synapomorphies for each node are given in Appendix 3. *Anchisaurus polyzelus* is nested at the base of the Sauropoda (Figure 13). This node is robust (decay index is 5, bootstrap frequency is 97%; Table 3). A Templeton test shows that the inclusion of *A. polyzelus* within the Sauropoda is a

significantly better explanation of the data than the shortest tree that includes *A. polyzelus* within the Prosauropoda (tree length 422) when compared to the most parsimonious tree that excludes *Efraasia minor* from the Prosauropoda ( $p = 0.0330$ ). When the shortest tree that includes *Anchisaurus polyzelus* in the Prosauropoda is compared to the other most-parsimonious tree (where *Efraasia minor* is included within the Prosauropoda), the result is not significant at the 0.05 level although it does approach it ( $p = 0.0956$ ). The results are similar if Ornithischia and an expanded Theropoda, inclusive of *Herrerasaurus ischigualastensis*, are used as outgroups. Once again, two most-parsimonious trees result (tree length 402, consistency index of 0.560, retention index of 0.726) and these are almost the

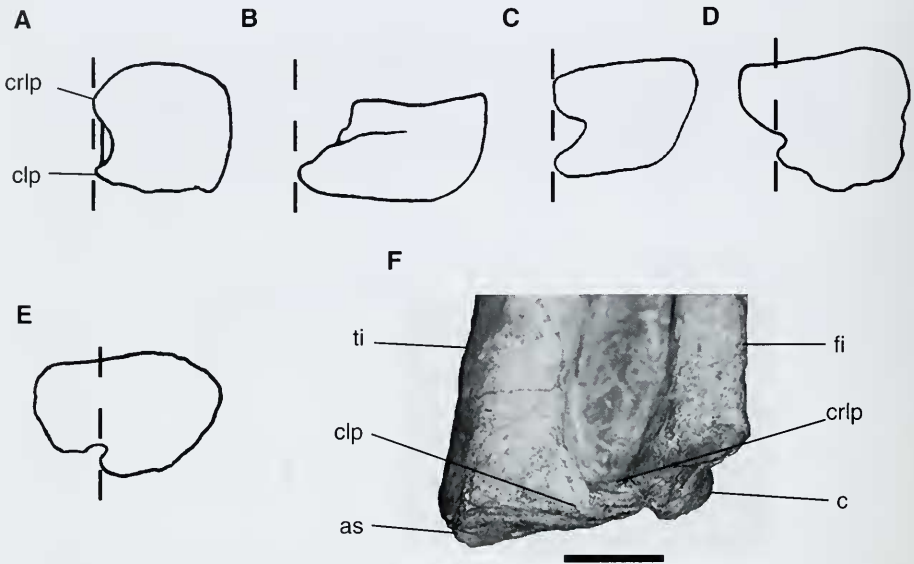


Figure 12

A–E, the right tibia of various saurischians in distal view showing the lateral extent of the caudolateral process. A, *Herrerasaurus ischigualastensis*, redrawn from Novas (1993); B, *Dilophosaurus wetherilli*, redrawn from Welles (1984); C, *Massospondylus carinatus*, redrawn from Cooper (1981); D, undescribed basal sauropod, BP/1/ 4952; E, *Camarasaurus grandis*, redrawn from Ostrom and McIntosh (1966). F, *Anchisaurus polyzelus*, YPM 1883, right lower leg and ankle in caudal view. D–F show the derived state for character 182. A–E not to scale, scale bar in F is 20 mm.

same as the first set. They differ in that *Efraasia minor* is resolved as the sister group to all other prosauropods in both trees and the position of *Thecodontosaurus* is variable (it is either the sister group of *Saturnalia tupiniquim* or all other sauropodomorphs). The robustness of the node connecting *Anchisaurus polyzelus* to all other sauropods is essentially undiminished (decay index is 5, bootstrap frequency is 94%). Thus the choice of outgroup exerts little influence on the position of *Anchisaurus polyzelus* within the tree.

### The Evolution of Body Size in Sauropodomorpha

To examine the evolution of sauropodomorph body size in the light of the phylogeny presented here, maximum femur lengths for each of the terminal taxa were coded as a continuous character in MacClade 4.0 (Maddison and Maddison 2000). Femur length was used because it is the best available proxy for body size that can be measured, or at least estimated, in all of the terminal taxa (Table 4). Ranges of taxa were used to represent the super-

specific terminals. These were selected to represent all of the main basal branches of the superspecific taxa. In the case of Theropoda they were *Megapnosaurus rhodesiensis*, *Liliensternus liliensterni*, *Dilophosaurus wetherilli*, *Ceratosaurus magnicornis*, *Elaphrosaurus bambergi* and *Siuraptor dongi*, whereas in Neosauropoda they were *Rayososaurus tessonei*, *Apatosaurus excelsus*, *Camarasaurus supremus* and *Brachiosaurus brancai*.

Two trees were constructed in MacClade using the two most-parsimonious trees from the present cladistic analysis (*Herrerasaurus* and Theropoda as outgroups) as a base. Tree A placed *Efraasia minor* as the sister group of Prosauropoda + Sauropoda, while tree B placed it as the sister group to all other prosauropods. Theropoda and Neosauropoda were replaced with the following topologies: (((*Megapnosaurus* + *Liliensternus*) + *Dilophosaurus*) + ((*Ceratosaurus* + *Elaphrosaurus*) + *Siuraptor*)) and ((*Rayososaurus* + *Apatosaurus*) + (*Camarasaurus* + *Brachiosaurus*)), respectively. The placement of Ceratosauria closer to Tetanurae than to Coelophysoidea follows Forster (1999), Rauhut (2000) and Carrano and others (2002); the rest of these relationships are not controversial. This was done only to allow the optimization process to estimate the basal condition of these clades; patterns of size change within them were not looked at.

Square change parsimony was then used to optimize femur length onto these phylogenies. The reconstructed ancestral values and the changes that occur on each branch are given in Table 5. To test for significant sustained trends in body size, the most recent common ancestor

(MRCA) method of Carrano (2000) was used. In this method, paired comparisons of femur length are made between the most recent common ancestor and all its descendants for each clade in the analysis. The number of increases and decreases within each clade were counted and analyzed using a one-sample sign test (Table 6).

The results for trees A and B are essentially the same. In both trees the basal branch of Sauropodomorpha involves a modest size decrease relative to its ancestor, but this is within one standard deviation of the mean change for all branches (Table 5). Thereafter there is an almost continual increase in the lineage that leads to Neosauropoda, which becomes particularly marked after the divergence of *Blikanasaurus*. The largest single-branch changes are the increases on the branches that support *Plateosaurus*, *Kotasaurus* + more derived sauropods and Neosauropoda and the decreases on the branches that support *Anchisaurus* and *Blikanasaurus*. The steady increase throughout the sauropod lineage is reflected by the MRCA comparisons. These show significant trends towards size increase within Sauropodomorpha and its included clades up to Prosauropoda + Sauropoda, followed by Sauropoda and its included clades up to *Vulcanodon* + Eusauropoda. The trend towards size increase is not significant in the basal branches of the Prosauropoda and becomes a nonsignificant trend towards size decrease in the Massospondylidae (Table 6). The fact that this trend is not significant in the MRCA comparisons is probably an artifact of small sample size (there are only three massospondylid terminal taxa in this analysis).

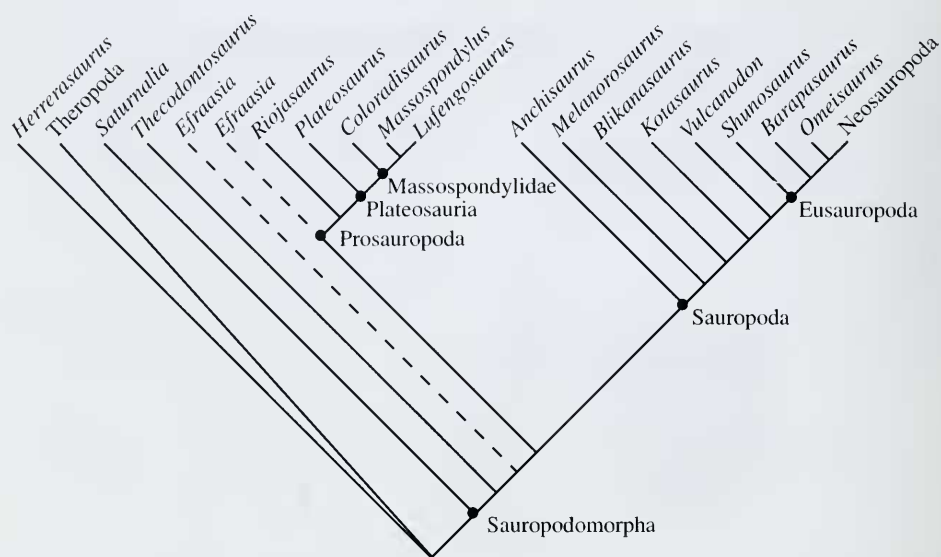


Figure 13

Sauropodomorph phylogeny based on the two most-parsimonious trees found in the cladistic analysis (using *Herrerasaurus* and *Theropoda* as outgroups). The dotted lines represent the alternative positions of the terminal taxon *Efraasia minor*.

## Discussion

The systematic status of the traditional prosauropod assemblage has been a contentious issue. Workers have supported either extreme paraphyly (Huene 1932; Romer 1956; Gauthier 1986; Benton 1990; Yates 2003a) or monophyly of the entire group (Cooper 1984; Galton 1990; Upchurch 1995; Sereno 1999; Benton and others 2000; Galton and Upchurch, in press). This analysis finds an intermediate hypothesis with a moderately diverse prosauropod clade. Nevertheless, it excludes many traditional members from the Prosauropoda, such as *Thecodontosaurus* spp., *Anchisaurus polyzelus*, *Melanorosaurus readi* and, in some cases,

*Efraasia minor*. Some of the character evidence that previously placed *Anchisaurus polyzelus* among prosauropods (such as a narrow, strap-like ventral process of the squamosal and ventrolateral rotation of the distal condyles of the first phalanx of manual digit 1 [Sereno 1999]) is weakened by the presence of the derived states for these characters in taxa (*Saturnalia tupiniquim* and *Thecodontosaurus* spp.) that seem to have diverged before the prosauropod–sauropod dichotomy.

The lineage that leads to the Neosauropoda shows a fairly continual increase in body size after the last common ancestor shared with *Saturnalia tupiniquim*. This lineage also displays an

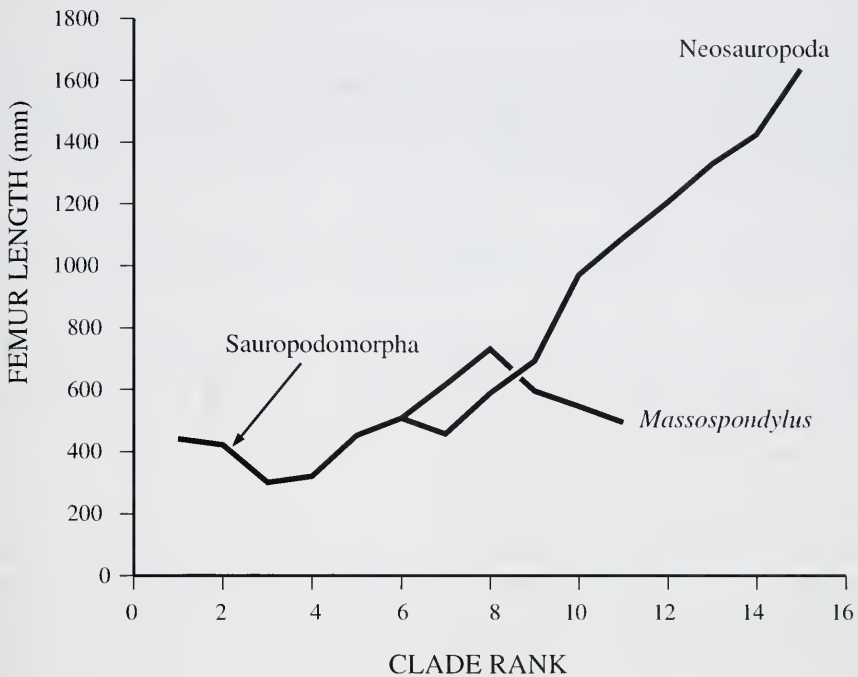


Figure 14

The evolution of femur length in two sauropodomorph lineages. Femur lengths are based on ancestral values calculated by square change parsimony (see Table 5). The arrow represents the origin of the Sauropodomorpha, immediately after its divergence from Theropoda.

accumulation of specializations towards herbivory. Early offshoots of this lineage (for example, *Thecodontosaurus*) were probably omnivorous (Kermack 1984), suggesting that this was the basal condition for the lineage (Barrett 2000), whereas neosauropods, and indeed all eusauropods, are undoubtedly strict herbivores. Thus, hypotheses where increased body size is coupled with increased commitment to herbivory (Farlow 1987; Barrett 2000) are supported. This coupling may be an example of “correlated progression” whereby a positive feedback loop

drives changes in multiple features of an organism towards increased specialization (Lee 1996). In this case an increase of plant matter in the diet would require a larger, heavier, gut to process it, which leads to an increase in body size and slower locomotion. This in turn, can lead to an increased vulnerability to predation, so a positive pressure to further increase size for protection is produced, which reduces the amount of nonplant material that the organism can procure. Thus the evolution of the lineage may become channeled towards the niche of gigantic,

Table 6

Results of the MRCA comparisons for both most parsimonious trees. Mean value of ancestor-descendant changes, with numbers of increases (+) and decreases (-), and the results of a one-sample sign test (n, sample size; p, probability). Asterisks indicate those results that are significant at the 0.05 level. *Clade abbreviations*: mdsn, more derived sauropodomorphs; mds, more derived sauropods; mde, more derived eusauropods.

| Clade                             | Mean         | +  | - | n  | p       |
|-----------------------------------|--------------|----|---|----|---------|
| <b>Tree A</b>                     |              |    |   |    |         |
| Saurischia                        | 390.9 ±536.1 | 22 | 5 | 27 | 0.001*  |
| Theropoda + Sauropodomorpha       | 423.8 ±541.5 | 22 | 4 | 26 | <0.001* |
| Sauropodomorpha                   | 638.7 ±578.1 | 17 | 3 | 20 | 0.001*  |
| <i>Thecodontosaurus</i> + mdsn    | 659.2 ±563.1 | 17 | 2 | 19 | 0.002*  |
| <i>Efraasia</i> + mdsn            | 570.5 ±546.7 | 17 | 1 | 18 | <0.001* |
| Prosauropoda + Sauropoda          | 542.8 ±548.9 | 15 | 2 | 17 | 0.001*  |
| Prosauropoda                      | 14.0 ±203.81 |    | 4 | 5  | 0.188   |
| Plateosauria                      | -97.2 ±234.9 | 1  | 3 | 4  | 0.625   |
| Massospondylidae                  | -77.7 ±31.20 |    | 3 | 3  | 0.125   |
| Sauropoda                         | 769.1 ±555.9 | 11 | 1 | 12 | 0.003*  |
| <i>Melanorosaurus</i> + mds       | 723.4 ±490.8 | 10 | 1 | 11 | 0.006*  |
| <i>Blikanasaurus</i> + mds        | 689.0 ±456.8 | 9  | 1 | 10 | 0.011*  |
| <i>Kotasaurus</i> + mds           | 506.6 ±362.2 | 9  | 0 | 9  | 0.002*  |
| <i>Vulcanodon</i> + Eusauropoda   | 429.1 ±361.0 | 8  | 0 | 8  | 0.004*  |
| Eusauropoda                       | 373.6 ±343.4 | 6  | 1 | 7  | 0.062   |
| <i>Barapasaurus</i> + mde         | 312.5 ±327.4 | 5  | 1 | 6  | 0.109   |
| <i>Omeisaurus</i> + Neosauropoda  | 275.0 ±331.7 | 4  | 1 | 5  | 0.188   |
| Neosauropoda                      | 160.5 ±286.4 | 3  | 1 | 4  | 0.625   |
| <b>Tree B</b>                     |              |    |   |    |         |
| Saurischia                        | 392.2 ±536.1 | 23 | 4 | 27 | <0.001* |
| Theropoda + Sauropodomorpha       | 426.4 ±541.5 | 22 | 4 | 26 | <0.001* |
| Sauropodomorpha                   | 644.0 ±578.1 | 17 | 3 | 20 | 0.001*  |
| <i>Thecodontosaurus</i> + mdsn    | 672.5 ±563.1 | 17 | 2 | 19 | 0.002*  |
| Prosauropoda + Sauropoda          | 605.1 ±546.7 | 17 | 1 | 18 | <0.001* |
| Prosauropoda                      | 91.4 ±187.2  | 4  | 2 | 6  | 0.344   |
| <i>Riojasaurus</i> + Plateosauria | 9.0 ±203.8   | 1  | 4 | 5  | 0.188   |
| Plateosauria                      | -99.1 ±234.9 | 1  | 3 | 4  | 0.625   |
| Massospondylidae                  | -78.4 ±31.2  | 0  | 3 | 3  | 0.125   |
| Sauropoda                         | 804.1 ±555.9 | 11 | 1 | 12 | 0.003*  |
| <i>Melanorosaurus</i> + mds       | 736.8 ±490.8 | 10 | 1 | 11 | 0.006*  |

Continued.



Table 6 continued

| Clade                            | Mean         | + | - | n  | p      |
|----------------------------------|--------------|---|---|----|--------|
| <b>Tree B continued</b>          |              |   |   |    |        |
| <i>Blikanasaurus</i> + mds       | 694.1 ±456.8 | 9 | 1 | 10 | 0.011* |
| <i>Kotasaurus</i> + mds          | 508.5 ±362.2 | 9 | 0 | 9  | 0.002* |
| <i>Vulcanodon</i> + Eusauropoda  | 430.1 ±361.0 | 8 | 0 | 8  | 0.004* |
| Eusauropoda                      | 374.6 ±343.4 | 6 | 1 | 7  | 0.062  |
| <i>Barapasaurus</i> + mde        | 313.5 ±327.4 | 5 | 1 | 6  | 0.109  |
| <i>Omeisaurus</i> + Neosauropoda | 275.0 ±331.7 | 4 | 1 | 5  | 0.188  |
| Neosauropoda                     | 160.5 ±286.4 | 3 | 1 | 4  | 0.625  |

graviportal herbivores. However, it is clear that not all sauropodomorphs were locked into correlated progression, neither was it an irreversible trend. It is notable that the lineage leading to Massospondylidae also involves the accumulation of specializations towards herbivory, since its divergence from the Sauropoda. These specializations include depression of the jaw joint below the tooth row, downturned dentary tip, restriction of the serrations of the teeth to the top half of the crowns (Appendix 3) and the possible development of a keratinous beak at the tip of the lower jaws (Crompton and Attridge 1986). Nevertheless, Prosauropoda do not show a sustained trend towards increasing size; indeed Massospondylidae show a trend towards size reduction. *Anchisaurus polyzelus* and *Blikanasaurus cromptoni* represent dramatic reversals of the trend towards increasing size within Sauropoda. The smaller specimen of *Anchisaurus polyzelus* (YPM 1883, femur length 211 mm), has closed neurocentral sutures in the trunk vertebrae. This indicates that it was mature or approaching maturity (Brochu 1996), and

therefore the larger YPM 208 (estimated femur length 275 mm) was probably an adult. Thus, despite its basal position, the species is almost half the size that is estimated for the common ancestor it shared with all other sauropods (Table 5).

Although it is the most basal sauropod known, *Anchisaurus polyzelus* was not the earliest. *Blikanasaurus cromptoni* is found to be a sauropod in this analysis as well as that of Galton and Upchurch (2003). The occurrence of *Blikanasaurus cromptoni* in the lower Elliot Formation (Galton and Heerden 1998) indicates that the sauropods were present in the Norian, whereas the occurrence of *Isanosaurus attavipachi* in the Nam Phong Formation (Buffetaut and others 2000) indicates that taxa close to the Eusauropoda (Wilson 2002, table 13), if not actually in it, existed before the close of the Triassic.

In conclusion, Prosauropoda is a moderately diverse clade of basal sauropodomorphs. Nevertheless, not all traditional prosauropods belong to it. In particular, *A. polyzelus* is actually a basal member of Sauropoda. The early evolu-

tion of the Sauropoda is characterized by a gradual and sustained size increase with some low-diversity offshoots that reversed this trend. *A. polyzelus* is one such early branch of the Sauropoda that became much smaller than its ancestors.

### Acknowledgments

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**Appendix 1**

## Character list.

1. Skull to femur ratio: greater than (0), or less than (1), 0.5 (Gauthier 1986).
2. Lateral plates appressed to the labial side of the premaxillary, maxillary and dentary teeth: absent (0) or present (1) (Upchurch 1995).
3. Distal end of the dorsal premaxillary process: tapered (0) or transversely expanded (1) (Sereno 1999).
4. Caudolateral process of premaxilla: present (0) or absent (1) (Sereno 1999; referring to variation within theropods).
5. Dorsal profile of the snout: straight to gently convex (0) or with a depression behind the naris (1).
6. Elongate median nasal depression: absent (0) or present (1) (Sereno 1999).
7. Relationship between caudolateral process of the premaxilla and the rostroventral process of the nasal: broad sutured contact (0), point contact (1) or separated by maxilla (2) (modified from Gauthier 1986). Ordered.
8. Ratio of narial diameter to orbital diameter: less than (0), or greater than (1), 0.5 (Wilson and Sereno 1998).
9. Narial position: near terminus of snout (0) or retracted caudodorsally so that the dorsal margin is level with the dorsal margin of the orbit (1) (Wilson and Sereno 1998).
10. Profile of premaxilla: convex (0) or with an inflection at the base of the dorsal process (1) (Upchurch 1995).
11. Rostrocaudal length of the antorbital fossa: greater (0), or less (1), than that of the orbit (Yates 2003a).
12. Rostral profile of the maxilla: slopes continuously towards the rostral tip (0) or with a strong inflection at the base of the ascending ramus, creating a rostral ramus with parallel dorsal and ventral margins (1) (Sereno and others 1996; referring to variation within theropods).
13. Length of rostral ramus of the maxilla: less than (0), or greater than (1), its dorsoventral depth (Sereno and others 1996; referring to variation within theropods).
14. Size of the neurovascular foramen at the caudal end of the lateral maxillary row: not larger than the others (0) or distinctly larger than the others in the row (1) (Yates 2003a).
15. Direction that the neurovascular foramen at the caudal end of the lateral maxillary

- 
- row opens: rostrally, ventrally, laterally (0) or caudally (1) (modified from Sereno 1999).
16. Arrangement of lateral maxillary neurovascular foramina: linear (0) or irregular (1) (modified from Sereno 1999).
17. Shape of the rostral margin of the antorbital fenestra: strongly concave, roughly parallel to the rostral margin of the antorbital fossa, creating a narrow antorbital fossa (0) or straight to gently concave creating a broad, subtriangular antorbital fossa (1) (Galton 1985a).
18. Dorsally open neurovascular canal on the floor of the antorbital fossa: absent (0) or present (1) (Yates 2003a).
19. Nasal contribution to the margin of the antorbital fenestra: absent (0) or present (1) (modified from Sereno 1999).
20. Pointed caudolateral process of the nasal overlapping the lacrimal: absent (0) or present (1) (Sereno 1999).
21. Dorsal exposure of the lacrimal: present (0) or absent (1) (Gauthier 1986).
22. Length of the rostral ramus of the lacrimal: greater than (0), or less than (1), half the length of the ventral ramus (modified from Galton 1990).
23. Extension of the antorbital fossa onto the ventral end of the lacrimal: present (0) or absent (1) (modified from Wilson and Sereno 1998).
24. Length of the caudal process of the prefrontal: short (0), or elongated (1), so that total prefrontal length is equal to the rostrocaudal diameter of the orbit (Galton 1985a).
25. Jugal contribution to the antorbital fenestra: absent (0) or present (1) (Holtz 1994).
26. Shape of the rostral end of the jugal: blunt (0) or sharply tapered (1) (Rauhut 2000).
27. Ratio of the minimum depth of the jugal below the orbit to the distance between the rostral end of the jugal and the rostroventral corner of the lower temporal fenestra: less than (0), or greater than (1), 0.2 (modified from Galton 1985a).
28. Transverse width of the ventral ramus of the postorbital: less than (0), or greater than (1), its rostrocaudal width at midshaft (Wilson and Sereno 1998).
29. Position of the rostral margin of the lower temporal fenestra: behind the orbit (0), extends under the rear half of the orbit (1) or extends as far forward as the midlength of the orbit (2) (modified from Upchurch 1995). Ordered.
30. Frontal contribution to the supratemporal fenestra: present (0) or absent (1) (modified from Gauthier 1986).
31. Orientation of the long axis of the supratemporal fenestra: longitudinal (0) or transverse (1) (Wilson and Sereno 1998).

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32. Length of the quadratojugal ramus of the squamosal relative to the width at its base: less than (0) or greater than (1) 4 times its width (Serenó 1999).
33. Squamosal–quadratojugal contact: present (0) or absent (1) (Gauthier 1986).
34. Angle of divergence between jugal and squamosal rami of quadratojugal: close to 90° (0) or close to parallel (1).
35. Length of jugal ramus of quadratojugal: no longer than (0), or longer than (1), the squamosal ramus (Wilson and Sereno 1998).
36. Shape of the rostral end of the jugal ramus of the quadratojugal: tapered (0) or dorsoventrally expanded (1) (Wilson and Sereno 1998).
37. Rounded, heel-like caudoventral process of the quadratojugal: absent (0) or present (1).
38. Position of the quadrate foramen: on the quadrate–quadratojugal suture (0) or deeply incised into, and partly encircled by, the quadrate (1) (Rauhut 2000).
39. Proportion of the length of the quadrate that is occupied by the pterygoid wing: at least 70% (0) or greater than 70% (1) (Yates 2003a).
40. Shape of jugal process of ectopterygoid: gently curved (0) or strongly recurved and hook-like (1) (Yates 2003a).
41. Pneumatic fossa on the ventral surface of the ectopterygoid: present (0) or absent (1) (Serenó and others 1996).
42. Position of the maxillary articular surface of the palatine: along the lateral margin of the bone (0) or at the end of a narrow anterolateral process (1) (Wilson and Sereno 1998).
43. Medial process of the pterygoid forming a hook around the basiptyergoid process: absent (0), flat and blunt-ended (1) or bent upwards and pointed (2) (modified from Wilson and Sereno 1998). Ordered.
44. Ridge formed along the junction of the parabasisphenoid and the basioccipital, between the basal tuberae: present with a smooth rostral face (0), present with a median fossa on the rostral face (1), or absent with the basal tuberae being separated by a deep caudally opening U-shaped fossa (2). Unordered.
45. Ossification of the extremity of the basal tuber: complete so that the basioccipital and parabasisphenoid form a single rugose tuber (0), or unossified with the basioccipital forming a ventrally facing platform of unfinished bone that abuts a similarly unfinished, caudally facing wall of the parabasisphenoid (1).
46. Shape of basal tuberae: knob-like, with basisphenoidal component rostral to basioccipital component (0), or forming a transverse ridge with the basisphenoidal component lateral to the basioccipital component (1).



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47. Dorsovenral depth of the parashenoid rostrum: much less than (0) or about equal to the transverse width (1) (Yates 2003a).
48. Deep septum spanning the interbasipterygoid space: absent (0) or present (1) (Galton 1990).
49. Shape of the floor of the braincase in lateral view: relatively straight with the basal tuberae, basipterygoid processes and parasphenoid rostrum roughly aligned (0), bent with the basipterygoid processes and the parasphenoid rostrum below the level of the basioccipital condyle and the basal tuberae (1), or bent with the basal tuberae lowered below the level of the basioccipital and the parasphenoid rostrum raised above it (2) (modified from Galton 1990). Unordered.
50. Length of the basipterygoid processes (from the top of the parasphenoid to the tip of the process): less than (0), or greater than (1), the height of the braincase (from the top of the parasphenoid to the top of the supraoccipital) (Benton and others 2000).
51. Location of the post-temporal fenestra: between the parietal, the supraoccipital and the exoccipital–opisthotic complex (0) or fully enclosed by the supraoccipital (1) (Yates 2003a).
52. Fontanelle between the supraoccipital and the parietals: absent (0) or present (1).
53. Shape of the supraoccipital: diamond-shaped, at least as high as wide (0), or semilunate and wider than high (1) (Yates 2003b).
54. Position of jaw joint: no lower than the level of the dorsal margin of the dentary (0) or depressed well below this level (1) (Serenó 1999).
55. Shape of upper jaws in ventral view: narrow with an acute rostral apex (0) or broad and U-shaped (1) (Wilson and Sereno 1998).
56. Caudal end of dentary tooth row medially inset with a thick lateral ridge on the dentary, forming a buccal emargination: absent (0) or present (1) (Gauthier 1986).
57. Orientation of the symphyseal end of the dentary: in line with the long axis of the dentary (0) or strongly curved ventrally (1) (Serenó 1999).
58. Position of first dentary tooth: adjacent to symphysis (0) or inset one tooth's width from the symphysis (1) (Serenó 1999).
59. Height (length ratio of the dentary): less than (0), or greater than (1), 0.2 (modified from Benton and others 2000).
60. Dorsovenral expansion at the symphyseal end of the dentary: absent (0) or present (1) (Wilson and Sereno 1998).
61. A stout, triangular, medial process of the articular, behind the glenoid: absent (0) or present (1) (Yates 2003a).
62. Length of the retroarticular process: less than (0), or greater than (1), than the depth

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of the mandible below the glenoid (Yates 2003a).

63. Strong medial embayment behind glenoid of the articular in dorsal view: absent (0), or present (1).

64. Orientation of the maxillary tooth crowns: erect (0) or procumbent (1) (modified from Gauthier 1986).

65. Orientation of the dentary tooth crowns: erect (0) or procumbent (1) (modified from Gauthier 1986).

66. Number of dentary teeth (in adults): less than 18 (0), 18 or more (1) (modified from Wilson and Sereno 1998).

67. Teeth with basally constricted crowns: absent (0) or present (1) (Gauthier 1986).

68. Tooth-tooth occlusion: absent (0) or present (1) (Wilson and Sereno 1998).

69. Mesial and distal serrations of the teeth: fine and set at right angles to the margin of the tooth (0) or coarse and angled upwards at an angle of 45° to the margin of the tooth (1) (Benton and others 2000).

70. Long axis of the tooth crowns distally recurved: present (0) or absent (1) (Gauthier 1986).

71. Texture of the enamel surface: smooth (0) or finely wrinkled (1) (Wilson and Sereno 1998).

72. Lingual concavities of the teeth: absent (0) or present (1) (Upchurch 1995).

73. Longitudinal labial grooves on the teeth: absent (0) or present (1) (Upchurch 1998).

74. Distribution of the serrations along the mesial and distal carinae of the tooth: extend along most of the length of the crown (0) or are restricted to the upper half of the crown (1) (Yates 2003a).

75. Shallow, dorsally facing fossa on the atlantal neurapophysis: absent (0) or present (1).

76. Posterior margin of the axial postzygapophyses: overhang the axial centrum (0) or are flush with the caudal face of the axial centrum (1) (Sereno 1999).

77. Dorsal excavation of the cervical parapophyses: absent (0) or present (1) (Upchurch 1998).

78. Strong lateral compression of the cranial cervical vertebrae: absent (0) or present (1) (Upchurch 1998).

79. Number of cervical vertebrae: 9 to 10 (0), 12 to 13 (1), or more than 13 (2) (Wilson and Sereno 1998). Ordered.

80. Length of the centrum of the third cervical vertebra: less than (0), or more than (1), 2.5 times the height of its cranial face (modified from Sereno 1999).

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81. Ventral keels on cranial cervical centra: present (0) or absent (1) (modified from Upchurch 1998).
82. Lamination of the cervical neural arches 4 to 8: well developed with a diapophyseal–postzygapophyseal lamina (0) or weakly developed with no diapophyseal–postzygapophyseal lamina (1) (Yates 2003a).
83. Short cranially projected pedicels bearing axial prezygapophyses: absent (0) or present (1) (Sereno 1999).
84. Epipophyses overhanging the rear margin of the postzygapophyses: absent (0), or present (1), in at least some postaxial cervical vertebrae (Sereno and Novas 1993).
85. Caudal ends of cranial, postaxial epipophyses: with a free pointed tip (0) or joined to the postzygapophysis along their entire length (1).
86. Cervical centra: amphicoelous (0) or opisthocoelous (1) (Gauthier 1986).
87. Lateral expanded tables at the midlength of the dorsal surface of the neural spines: absent in all vertebrae (0), present on the pectoral vertebrae (1) or present on the pectoral and cervical vertebrae (2). Ordered.
88. Dorsoventral height of the hyposphenes: much less than (0), or equal to (1), the dorsoventral height of the neural canal.
89. Height of the dorsal neural spines: greater than (0), or less than (1), 1.5 times the length of the base of the spine (modified from Bonaparte 1986).
90. Lateral surfaces of the dorsal centra: with at most vague, shallow depressions (0), with deep fossae that approach the midline (1), or with invasive, sharp-rimmed pleurocoels (2) (Gauthier 1986). Ordered.
91. Diapo-prezygapophyseal lamina and associated anterior triangular fossa (chonos): present on all dorsals (0) or absent in mid-dorsals (1) (Yates 2003a).
92. Cross-sectional shape of dorsal neural spines: narrow and elliptical (0) or broad and triangular (1) (Bonaparte 1986).
93. Composite lateral spinal laminae on dorsal neural spines: absent (0) or present (1) (Wilson and Sereno 1998).
94. Dorsal centra: entirely amphicoelous to amphiplatyan (0), first two dorsals are opisthocoelous (1), or cranial half of dorsal column is opisthocoelous (2) (Wilson and Sereno 1998). Ordered.
95. Excavations of the cranial face of the dorsal neural arches, surrounding the neural canal: absent (0) or present (1).
96. Well-developed suprapostzygapophyseal laminae: absent (0), or present on at least the caudal dorsal vertebrae (1) (Bonaparte 1986).

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97. Supradiapophyseal laminae on dorsal vertebrae: absent (0) or present (1).
  98. Accessory infrapostzygapophyseal lamina in dorsal vertebrae: present (0) or absent (1).
  99. Last presacral rib: free (0) or fused to vertebra (1).
  100. Caudosacral vertebra: absent (0) or present (1) (Galton and Upchurch, in press)
  101. Number of dorsosacral vertebrae: none (0), one (1), or two (2) (modified Gauthier 1986).
  102. Strong constriction between the sacral rib and the transverse process of the first primordial sacral rib (and dorsosacral if present) in dorsal view: absent (0) or present (1).
  103. Length of first caudal centrum: less than (0), or greater than (1), its height (Yates 2003a).
  104. Length of base of the proximal caudal neural spines: less than (0), or greater than (1), half the length of the neural arch (Gauthier 1986).
  105. Position of postzygapophyses in proximal caudal vertebrae: protruding with an interpostzygapophyseal notch visible in dorsal view (0) or placed on either side of the caudal end of the base of the neural spine without any interpostzygapophyseal notch (1) (Yates 2003a).
  106. A hyposphenal ridge on caudal vertebrae: absent (0) or present (1) (Upchurch 1995).
  107. Midcaudal chevrons with a ventral slit: absent (0) or present (1) (Upchurch 1995).
  108. Length of midcaudal centra: greater than (0), or less than (1), twice the height of their anterior faces (Yates 2003a).
  109. Longitudinal ventral sulcus on caudal centra: absent (0) or present (1) (Upchurch 1995).
  110. Length of the longest chevron: less than (0), or greater than (1), the length of the preceding centrum (Yates 2003a).
  111. Longitudinal ridge on the dorsal surface of the sternal plate: absent (0) or present (1) (Upchurch 1998).
  112. Craniocaudal length of the acromion process of the scapula: less than (0), or greater than (1), 1.5 times the minimum width of the scapula blade (Wilson and Sereno 1998).
  113. Minimum width of the scapula: less than (0), or greater than (1), 20% of its length (Gauthier 1986).
  114. Scapula blade in lateral view: with a strap-shaped midsection that has straight, subparallel margins (0) or waisted with curved margins (1) (Sereno and others 1993).
  115. Caudal margin of the acromion process of the scapula: rises from the blade at

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angle that is less than (0), or greater than (1), 65° from the long axis of the scapula, at its steepest point (modified from Novas 1992).

116. Flat caudoventrally facing surface on the coracoid between glenoid and coracoid tubercle: absent (0) or present (1).

117. Coracoid tubercle: present (0) or absent (1) (modified from Pérez-Moreno and others 1994; referring to variation within theropods).

118. Length of the deltopectoral crest of the humerus: less than (0), or greater than (1), 50% of the length of the humerus (Serenó 1999).

119. Deltopectoral crest of the humerus: a tall, sharp-edged crest (0) or a low, rounded ridge (1) (Wilson and Sereno 1998).

120. Length of the humerus: less than 55% (0), 55 to 65% (1), or greater than 65% (2), of the length of the femur (modified from Gauthier 1986). Ordered.

121. Craniolateral margin of the deltopectoral crest of the humerus: straight (0) or strongly sinuous (1) (Yates 2003a).

122. Well-defined fossa on the distal flexor surface of the humerus: present (0) or absent (1).

123. Transverse width of the distal humerus: less than (0), or greater than (1), 33% of the length of the humerus (Langer 2001).

124. Length of the radius: less than (0), or greater than (1), 80% of the humerus (modified from Langer 2001).

125. Deep radial fossa on proximal ulna: absent (0) or present (1) (Wilson and Sereno 1998).

126. Olecranon process on proximal ulna: present (0) or absent (1) (Wilson and Sereno 1998).

127. Maximum linear dimensions of the ulnare and radiale: exceed that of at least one of the first three distal carpals (0) or are less than any of the distal carpals (1) (Yates 2003a).

128. Transverse width of the first distal carpal: less than (0), or greater than (1), 120% of the transverse width of the second distal carpal (Serenó 1999).

129. Lateral end of first distal carpal: abuts (0), or overlaps (1), second distal carpal (Yates 2003a).

130. Proximal end of first metacarpal: flush with other metacarpals (0) or inset into the carpus (1) (Serenó 1999).

131. Second distal carpal: does (0), or does not (1), completely cover the proximal end of the second metacarpal.

132. Length of the manus: greater than 45% (0), between 45 and 38% (1), or less than 38% (2), of the humerus + radius (modified from Sereno and others 1993). Ordered.



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133. Proximal width of first metacarpal: less than (0), or greater than (1), the proximal width of the second metacarpal (modified from Gauthier 1986).
134. Proximal width of the first metacarpal: less than 65% (0), between 65% and 80% (1), or greater than 80% (2), of its length (modified from Sereno 1999). Ordered.
135. Strong assymetry in the lateral and medial distal condyles of the first metacarpal: absent (0) or present (1) (Gauthier 1986).
136. Shape of the fifth metacarpal: longer than wide at the proximal end with a flat proximal surface (0) or close to as wide as it is long with a strongly convex proximal articulation surface (1) (Yates 2003a).
137. Length of the fifth metacarpal: less than (0), or greater than (1), 75% of the length of the third metacarpal (Upchurch 1998).
138. Deep distal extensor pits on the second and third metacarpals: present (0) or absent (1) (Novas 1993).
139. Ventrolateral twisting of the transverse axis of the distal end of the first phalanx of manual digit one relative to its proximal end: absent (0), present but much less than 60° (1), or 60° (2) (Sereno 1999). Ordered.
140. Length of manual digit one: less than (0), or greater than (1), the length of manual digit two (Yates 2003a).
141. Length of the ungual of manual digit 2: greater than the length of the ungual of manual digit 1 (0), 75% to 100% of the ungual of manual digit 1 (1), less than 75% of the ungual of manual digit 1 (2), or the ungual of manual digit 2 absent (3) (modified from Gauthier 1986). Ordered.
142. Shape of nonterminal manual phalanges: longer than wide (0) or as long as wide (1) (Yates 2003a).
143. Phalangeal formula of manual digits IV and V: greater than (0), or less than (1), 2–0, respectively (Gauthier 1986).
144. Strongly convex dorsal margin of the ilium: absent (0) or present (1) (Gauthier 1986).
145. Cranial extent of preacetabular process of ilium: does not (0), or does (1), project further forward than cranial end of the pubic peduncle (Yates 2003a).
146. Buttress between preacetabular process and the supra-acetabular crest of the ilium: present (0) or absent (1) (Yates 2003a).
147. Shape of the preacetabular process: blunt and rectangular (0) or with a pointed, projecting cranioventral corner and a rounded dorsum (1) (modified from Sereno 1999).
148. Length of the postacetabular process of the ilium: greater than (0), or less than (1), 30% of the total length of the ilium.

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149. Depth of the preacetabular process of the ilium: much less than (0), or subequal to (1), the depth of the ilium above the acetabulum (modified from Gauthier 1986).
150. Length of preacetabular process of the ilium: less than (0), or greater than (1), twice its depth.
151. Medial bony wall of the acetabulum: at least partially present (0) or absent (1) (Gauthier 1986).
152. Well-developed brevis fossa with sharp margins on the ventral surface of the postacetabular process of the ilium: absent (0) or present (1) (Gauthier 1986).
153. Length of the pubic peduncle of the ilium: less than (0), or greater than (1), twice the craniocaudal width of its distal end (Serenio 1999).
154. Caudally projecting "heel" at the distal end of the ischial peduncle: absent (0) or present (1) (Yates 2003b).
155. Length of the ischial peduncle of the ilium: similar to (0), or much shorter than (1), the pubic peduncle (Wilson and Sereno 1998).
156. Shape of the caudal margin of the postacetabular process of the ilium: rounded to bluntly pointed (0), square ended (1), or with a pointed ventral corner and a rounded caudodorsal margin (2) (Yates 2003b). Unordered.
157. Notch separating caudoventral end of the ischial obturator plate from the ischial shaft: present (0) or absent (1) (Rauhut 2000; referring to variation within theropods).
158. Elongate interischial fenestra: absent (0) or present (1) (Yates 2003b).
159. Length of ischium: less than (0) or greater than (1) that of the pubis (Salgado and others 1997).
160. Shape of the transverse section of the ischial shaft: ovoid to subrectangular (0) or triangular (1) (Serenio 1999).
161. Orientation of the long axes of the transverse section of the distal ischia: meet at an angle (0) or are colinear (1) (Wilson and Sereno 1998).
162. Depth of the transverse section of the ischial shaft: at least as great as (0), or much less than (1), the transverse width of the section (Wilson and Sereno 1998).
163. Transverse width of the conjoined distal ischial expansions: greater than (0), or less than (1), their sagittal depth (Yates 2003a).
164. Pubic tubercle on the lateral surface of the proximal pubis: present (0) or absent (1) (Yates 2003a).
165. Width of the conjoined pubes: less than (0), or greater than (1), 75% of their length (Cooper 1984).

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166. Lateral margins of the pubic apron in cranial view: straight (0) or concave (1).
167. Orientation of the pubic blades: transverse (0) or twisted posteromedially (1) (Wilson and Sereno 1998).
168. Minimum transverse width of the pubic apron: much more than (0), or less than (1), 40% of the width across the iliac peduncles of the ilium.
169. Craniocaudal length of the distal pubic expansion: less than (0), or greater than (1), 15% of the length of the pubis (modified from Gauthier 1986; referring to variation within theropods).
170. Length of the hind limb: greater than (0), or less than (1), the length of the trunk (Gauthier 1986).
171. Longitudinal axis of the femur in lateral view: strongly bent with an offset between the proximal and distal axes greater than  $15^\circ$  (0), weakly bent with an offset of less than  $10^\circ$  (1), or straight (2) (Cooper 1984). Ordered.
172. Shape of the cross section of the midshaft of the femur: subcircular (0) or strongly elliptical with the long axis oriented mediolaterally (1) (Wilson and Sereno 1998).
173. Height of the fourth trochanter: tall crest (0) or a low rugose ridge (1) (Gauthier 1986).
174. Shape of the lesser trochanter: small rounded tubercle (0), elongate ridge oriented dorsoventrally (1), or absent (2) (modified from Gauthier 1986). Unordered.
175. Angle between the long axis of the femoral head and the transverse axis of the distal femur: about  $30^\circ$  (0) or close to  $0^\circ$  (1) (Carrano 2000).
176. Shelf-like ridge associated with lesser trochanter: present (0) or absent (1).
177. Position of the fourth trochanter along the length of the femur: in the proximal half (0) or straddling the midpoint (1) (Galton 1990).
178. Profile of the fourth trochanter of the femur: rounded and symmetrical (0) or asymmetrical with a steeper distal slope than the proximal slope and a distinct distal corner (1) (Langer 2001).
179. Position of fourth trochanter along the mediolateral axis of the femur: centrally located (0) or on the medial margin (1) (Galton 1990).
180. Tibia (femur length ratio): greater than 1.0 (0), between 1.0 and 0.6 (1), or less than 0.6 (2) (modified from Gauthier 1986). Ordered.
181. Extensor depression on the distal femur: absent (0) or present (1) (Molnar and others, 1990; referring to variation within theropods).
182. Lateral margin of descending caudoventral process of the distal tibia: protrudes laterally at least as far as (0), or set well back from (1), the craniolateral corner of the distal tibia.

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183. Transverse width of the distal tibia: subequal to (0), or greater than (1), its craniocaudal length (Gauthier 1986).
184. A triangular rugose area on the medial side of the fibula: absent (0) or present (1).
185. Ossified distal tarsals: present (0) or absent (1) (Gauthier 1986).
186. Depth of the medial end of the astragalar body in cranial view: roughly equal to the lateral end (0) or much shallower creating a wedge shaped astragalar body (Wilson and Sereno 1998).
187. Shape of the caudomedial margin of the astragalus in dorsal view: forming a moderately sharp corner of a subrectangular astragalus (0) or evenly rounded, without forming a caudomedial corner (1) (Wilson and Sereno 1998).
188. Dorsally facing horizontal shelf forming part of the fibular facet of the astragalus: present (0) or absent with a largely vertical fibular facet (1) (Sereno 1999).
189. Vascular foramina set in a fossa at the base of the ascending process of the astragalus: present (0) or absent (1) (Wilson and Sereno 1998).
190. A lateral horizontal groove on the calcaneum: absent (0) or present (1).
191. Transverse width of the calcaneum: greater than (0), or less than (1), 30% of the transverse width of the astragalus.
192. Length of the third metatarsal: greater than (0), or less than (1), 40% of the length of the tibia (Gauthier 1986).
193. Proximal width of the first metatarsal: less than (0), or at least as great as (1), the proximal width of the second metatarsal (modified from Wilson and Sereno 1998).
194. Shape of the medial margin of the proximal surface of the second metatarsal: straight (0) or concave (1) (modified from Sereno 1999).
195. Shape of the lateral margin of the proximal surface of the second metatarsal: straight (0) or concave (1) (modified from Sereno 1999).
196. Transverse width of the proximal end of the fourth metatarsal: less than (0), or at least (1), twice the craniocaudal depth of the proximal end (modified from Sereno 1999).
197. Transverse width of the proximal end of the fifth metatarsal: less than 25% (0), between 30% and 49% (1), or greater than 50% (2), of the length of the fifth metatarsal (modified from Sereno 1999). Ordered.
198. Length of the ungual of pedal digit 2: greater than (0), between 100% and 90% (1), or less than 90% (2) of the length of the ungual of pedal digit 1 (modified from Gauthier 1986). Ordered.
199. Length of the first phalanx of pedal digit 1: greater than (0), or less than (1), the length of the ungual of pedal digit 1.

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200. Minimum shaft diameters of third and fourth metatarsals: greater than (0), or less than (1), 60% of the minimum shaft diameter of the second metatarsal (Wilson and Sereno 1998).

201. Shape of the ungual of pedal digit 1: shallow, pointed, with convex sides and a broad ventral surface (0), or deep, abruptly tapering, with flattened sides and a narrow ventral surface (1) (Wilson and Sereno 1998).

202. Size of the ungual of pedal digit 3: greater than (0), or less than (1), 85% of the ungual of pedal digit two in all linear dimensions (Yates 2003a).

203. Number of phalanges in pedal digit 4: five (0) or fewer than five (1) (Gauthier 1986).

204. Phalanges of pedal digit 5: absent (0) or present (1) (modified Gauthier 1986).

205. Pedal digit 5: reduced, nonweight-bearing (0), or large (fifth metatarsal at least 70% of fourth metatarsal), robust and weight bearing (1) (Wilson and Sereno 1998).



Appendix 2

Character–taxon matrix.

*Herrerasaurus ischigualastensis*

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00?1001??00000010000000000100000000000  
00000000000??10000000?000000001010000000000000001000000?10

Theropoda (excluding *Herrerasaurus*)

00(01)00020000(01)001000010000(01)1000000(01)0001(01)0100000000000000000000000  
0000000000000000000010100000010000000001(12)000000010000(01)000000000000  
10000000?0000(12)00011001011000100000001000100000?0000000010000000100?0000  
0000000

Theropoda (including *Herrerasaurus*)

000000(02)0000000(01)0000(01)00000(01)(01)00000000(01)00(01)000000000000000  
000000000000000000000000(01)0(01)000000(01)00000000(01)(012)0000000(01)00(01  
)00(01)00000000(01)000(01)000000(01)00000(012)000(01)(01)00(01)0(01)(01)000(01)  
000(01)000(01)000(01)00000000(01)0(01)00(01)0000000(01)0000(01)0000000(01)0

Ornithischia

00000000001000000000?0000000000(01)00000000010000000000(01)0(01)000010000  
1111100000000000?0(01)000010?000000?01(12)0000000000000100010000000000020  
000010000101110010110001000000100??00000?0101000010000?00000000000000000

*Saturnalia tupiniquim*

10????????????000?????????1?????00?????00?0000?????00010???00010010000??00???1???00  
01010000001000011????????101110001001000?????????????????????0?0?00?01100211010100000  
00100000001010000000000000010?00?0000

*Thecodontosaurus* spp.

10??00?00??(01)(01)0?1000000?100?00????0(01)0100000100010?100(01)01100000011  
0110000(01)?0000111000001010000000?00111100000?00001000?001000110000101000  
10100001100000100111?(01)0(01)0??000??000101010?000000010??0011111000?000

*Efraasia minor*

1010?11?00?11??0?00000?10??0?1????000??00101010?1101010011?00110110000?1000  
111?1000010?0000001001111000101?001010102001000111?00111001101010011000111  
00111010000000000000101010100100001?1000??1111000010

Continued.

*Riojasaurus incertus*

10?00??1001111101?00?001010?1001000000????1101?100?100000?011010011011000001  
00?011?10010101000000110110000010?00101010211100011111?1111011021?0011000  
111102010100010000010001110111101000010?0011121100?00

*Plateosaurus engelhardti*

1010111100011110111100010110000101000010101101011011010111001110011011000  
0110001110(01)0020101000000111011000011100010101010010001111111110120101  
00110001011020001001000000000010101011010000101000101111000010

*Coloradisaurus brevis*

?0101?2100?1111011????001110?0010100?01?01101111011010111001110011011000010  
00?1010000?0101000000110110010????000110101101????????????????????00110001?110?1  
111001101001?0001110111101??00100?00111221001010

*Massospondylus carinatus*

10101121001101100?1101010110100100100????00101100011010111001010(01)110110  
0011?00010101002010100000011011(01)0000011?000(01)10101001000111111211012  
120100110001010001101001101001100011101011010000101000111221001010

*Lufengosaurus huenei*

10?01121001111100???1101111?100101?0??010110?0?0?010???0011?0111011000???000  
101???0?0101000000?0011000?0111000111010110100011111121101212110011000101  
00211010001010011000111010110100001?1000111221001010

*Anchisaurus polyzelus*

10?0????0011111?01???1101112101?????1?0???2101020011101?0001001?010111?0110??0  
?01010?0010100?00??010?????????100(01)??002010000???1?2111101202010(01)1100110  
100?11?011010001010001110(01)11111?000?010?????111000000

*Melanorosaurus readi*

??00??11???00100100000  
01?1100000?10?0100??102010010??????21?????????0011000101001???1000100001?100111  
00111110?0010??01111??0?????

*Blikanasaurus cromptoni*

??  
??1?0011101111121  
11000?0

*Kotasaurus yamanpalliensis*

??1??1111??0?0001??101011001  
0?0??11?00?101??0000?00?01011????????????????????01110011010101?1?0??1????1?2111110  
0111110?1111??11????21?01???

*Vulcanodon karibaensis*

??1????????????????????1?  
???010?01??101??012010111????????????????????????10101?1111010100011?111111112??11  
111110111101221011?11

*Barapasaurus tagorei*

??1?11111???0?1?0??101010111  
121??11000?1??0??010101?1?????11????????????????1111110101010??11010110111?211211  
11?????1????????????????????

*Shunosaurus lii*

1101002111100002?001110001020001011111??12210?02000101000011001111111111  
?1?1100001110?011101?21?011?0001110?1?01?010120111?11000?21?01101311111110  
101010111101011?111121121100021?1?10?110111100221011111

*Omeisaurus tianfuensis*

11010021111100012?001110101?21101011111??1??1?00?00011100001?011011111111?0  
111100011101020112121??12000011101110110101201001????0?2001011????111111010  
1010111?0??110111121121110021??1?0011??1110022111?111

*Neosauropoda*

110100211(01)1(01)010120001110(01)011211010111110112210002(01)001110000110  
011011111(01)11(01)01011100111010201121211012000010101010010101201(01)0111  
1000200001101311111110101010111(01)1101101111211211101211111111101110002  
21111111

### Appendix 3

Tree description. For the sake of space, only one of the two most-parsimonious trees is described. In this tree *Efraasia* is the sister group to Prosauropoda + Sauropoda. For all simple 0 to 1 state changes only the character number is given; for all others the type of change is specified in parentheses.

#### Sauropodomorpha sensu lato

Unambiguous: 1, 32, 67, 70, 82, 89, 91, 103, 104, 120, 123, 153.

ACCTRAN: 3, 8, 11, 12, 13, 18, 29, 46, 52, 53, 59, 75, 76, 98, 114, 116, 127, 133, 139, 147, 157, 158, 170, 198.

#### *Thecodontosaurus* + (*Efraasia* + (Prosauropoda + Sauropoda))

Unambiguous: 58, 66, 69, 102, 174, 176, 188, 194, 195, 197.

ACCTRAN: 14, 15, 50, 56, 120 (1 to 2), 146, 190.

DELTRAN: 18, 46, 53, 127, 133, 139, 146, 147, 198.

#### *Efraasia* + (Prosauropoda + Sauropoda)

Unambiguous: 54, 61, 84, 101, 108, 110, 134, 138, 143, 151, 183, 199.

ACCTRAN: 6, 41, 43, 48, 59 (1 to 0), 118, 129, 130, 204.

DELTRAN: 12, 13, 98, 120 (1 to 2).

#### Prosauropoda + Sauropoda (= Sauropodomorpha sensu Sereno, 1998)

Unambiguous: 39, 103 (1 to 0), 104 (1 to 0), 132, 141 (1 to 2), 164, 175, 180.

ACCTRAN: 7 (1 to 2), 24, 27, 44, 50 (1 to 0), 122, 136, 139 (1 to 2), 179, 197 (1 to 2).

DELTRAN: 8, 11, 29, 41, 43, 170.

#### Prosauropoda

Unambiguous: 17, 53 (1 to 0), 63, 87, 99, 131, 154, 156 (1 to 2).

ACCTRAN: 51, 121, 157 (1 to 0).

DELTRAN: 14, 15, 24, 44, 48, 52, 118, 129, 130, 136.

#### Plateosauria

Unambiguous: 5, 19, 20, 34, 57, 62, 80, 87 (1 to 2), 109, 120 (2 to 1), 163.

ACCTRAN: 49, 122 (1 to 0), 179 (1 to 0).

DELTRAN: 3, 6, 27, 51, 56, 75, 139 (1 to 2), 204.

#### Massospondylidae

Unambiguous: 47, 81 (1 to 0), 115, 166, 169, 198 (1 to 2), 202.

ACCTRAN: 22, 25, 76 (1 to 0), 114 (1 to 0), 134 (1 to 2), 140, 157.

DELTRAN: 7 (1 to 2), 197 (1 to 2).

*Lufengosaurus* + *Massospondylus*

Unambiguous: 17 (1 to 0), 48 (1 to 0), 154 (1 to 0).

ACCTRAN: 35, 49 (1 to 0), 65, 74.

DELTRAN: 22, 134 (1 to 2), 140, 190.

## Sauropoda

Unambiguous: 22, 23, 29 (1 to 2), 38, 45, 46 (1 to 0), 49 (0 to 2), 58 (1 to 0), 64, 71, 74, 102 (1 to 0), 123 (1 to 0), 132 (1 to 2), 182, 191.

ACCTRAN: 3 (1 to 0), 6 (1 to 0), 21, 28, 30, 33, 35, 36, 37, 42, 43 (1 to 2), 44 (1 to 2), 48 (1 to 0), 65, 66 (1 to 0), 72, 76 (1 to 0), 81 (1 to 0), 111, 114 (1 to 0), 116 (1 to 0), 117, 118 (1 to 0), 129 (1 to 0), 159, 162, 168, 178 (1 to 0), 190 (1 to 0), 193.

DELTRAN: 27, 44 (0 to 2), 122, 179.

*Melanorosaurus* + (*Blikanasaurus* + (*Kotasaurus* + (*Vulcanodon* + Eusauropoda)))

Unambiguous: 88, 89 (1 to 0), 100, 125, 169.

ACCTRAN: 2, 4, 9, 10, 13 (1 to 0), 14 (1 to 0), 15 (1 to 0), 17 (0 to 2), 18 (1 to 0), 24 (1 to 0), 26 (1 to 0), 32 (1 to 0), 52 (1 to 0), 55, 56 (1 to 0), 60, 68, 73, 79, 85, 130 (1 to 0), 136 (1 to 0), 137, 139 (2 to 0), 140, 141 (2 to 3), 142, 171.

DELTRAN: 178 (1 to 0), 193.

*Blikanasaurus* + (*Kotasaurus* + (*Vulcanodon* + Eusauropoda))

Unambiguous: 187, 189, 192.

ACCTRAN: 77, 82 (1 to 0), 86, 90, 94, 96 (0 to 2), 106, 124, 126, 145, 155, 156 (1 to 0), 171 (1 to 2), 172, 173.

DELTRAN: 197 (1 to 2).

*Kotasaurus* + (*Vulcanodon* + Eusauropoda)

Unambiguous: 198 (1 to 2), 202.

ACCTRAN: 185, 186, 195 (1 to 0), 203, 205.

DELTRAN: 72, 73, 82 (1 to 0), 86, 90, 94, 106, 124, 145, 155, 156 (1 to 0), 159, 171 (0 to 2), 172, 173.

*Vulcanodon* + Eusauropoda

Unambiguous: 115, 119, 180 (1 to 2), 184, 201.

ACCTRAN: 92, 95, 97, 144, 148, 149, 177.

DELTRAN: 126, 162, 168, 185, 195 (1 to 0), 204, 205.

## Eusauropoda

Unambiguous: 165, 167, 174 (1 to 2), 196 (1 to 0).

ACCTRAN: 107, 179 (1 to 0), 186 (1 to 0).

*Continued.*



DELTRAN: 2, 4, 7 (1 to 2), 9, 10, 13 (1 to 0), 17 (0 to 2), 21, 26 (1 to 0), 32 (1 to 0), 33, 35, 36, 37, 42, 43 (1 to 2), 55, 60, 65, 68, 79, 85, 92, 96 (0 to 2), 97, 116 (1 to 0), 117, 137, 139 (1 to 0), 140, 141 (2 to 3), 142, 144, 148, 149, 203.

*Barapasaurus* + (*Omeisaurus* + Neosauropoda)

Unambiguous: 80, 91 (1 to 0), 93.

ACCTRAN: 16, 25, 31, 124 (1 to 0), 133 (1 to 0), 134 (1 to 0), 200.

DELTRAN: 95, 177.

*Omeisaurus* + Neosauropoda

Unambiguous: 90 (1 to 2), 94 (1 to 2), 101 (1 to 2), 112.

DELTRAN: 16, 30, 31, 66 (1 to 0), 77, 124 (1 to 0), 133 (1 to 0), 134 (1 to 0), 200.

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**Literature Cited**

- Barrett, P. M.** 2000. Prosauropod dinosaurs and iguanas: speculations on the diets of extinct reptiles. In: H-D. Sues, ed. *Evolution of herbivory in terrestrial vertebrates*. Cambridge: Cambridge Univ. Pr. pp. 42–78.
- Benton, M. J.** 1990. Origin and interrelationships of dinosaurs. In: D. B. Weishampel, P. Dodson, and H. Osmólska, eds. *The Dinosauria*. Berkeley: Univ. California Pr. pp. 11–30.
- Benton, M. J., L. Juul, G. W. Storrs and P. M. Galton.** 2000. Anatomy and systematics of the prosauropod dinosaur *Thecodontosaurus antiquus* from the Upper Triassic of southwest England. *J. Vert. Paleontol.* 20:77–108.
- Berman, D. S. and J. S. McIntosh.** 1978. Skull and relationships of the Upper Jurassic sauropod *Apatosaurus* (Reptilia, Saurischia). *Bull. Carnegie Mus. Nat. Hist.* 8:1–35.
- Bonaparte, J. F.** 1972. Los tetrápodos del sector superior de la Formación Los Colorados, La Rioja, Argentina (Triásico Superior). I Parte. *Opera Lilloana* 22:1–183.
- 1978. *Coloradia brevis* n. g. et n. sp. (Saurischia, Prosauropoda), dinosaurio Plateosauridae superior de la Formación Los Colorados, Triásico Superior de La Rioja, Argentina. *Ameghiniana* 15:327–332.
- 1986. The early radiation and phylogenetic relationships of the Jurassic sauropod dinosaurs, based on vertebral anatomy. In: K. Padian, ed. *The beginning of the age of dinosaurs*. Cambridge: Cambridge Univ. Pr. pp. 247–258.
- Bonaparte, J. F., J. Ferigolo and A. M. Ribeiro.** 1999. A new early Late Triassic saurischian dinosaur from Rio Grande Do Sul State, Brazil. In: Y. Tomida, T. H. Rich and P. Vickers-Rich, eds. *Proceedings of the Second Gondwana Dinosaur Symposium*. pp. 89–109. (Natl. Sci. Mus. Monogr. 15).
- Bonaparte, J. F. and J. A. Pumares.** 1995. Notas sobre el primer craneo de *Riojasaurus incertus* (Dinosauria, Prosauropoda, Melanorosauridae) del Triasico Superior de La Rioja, Argentina. *Ameghiniana* 32:341–349.
- Bonaparte, J. F. and M. Vince.** 1979. El hallazgo del primer nido dinosaurios Triasicos, (Saurischia, Prosauropoda), Triasico Superior de Patagonia, Argentina. *Ameghiniana* 16:173–182.
- Bonnan, M. F.** 2000. The presence of a calcaneum in a diplodocid sauropod. *J. Vert. Paleontol.* 20:317–323.
- Britt, B. B.** 1991. Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. *Brigham Young Univ. Geol. Stud.* 37:1–72.
- Brochu, C. A.** 1996. Closure of neurocentral sutures during crocodylian ontogeny: implications for maturity assessment in fossil archosaurs. *J. Vert. Paleontol.* 16:49–62.

- Buffetaut, E., V. Suteethorn, G. Cuny, H. Tong, J. Le Loeuff, S. Khansubha and S. Jongautchariyakul.** 2000. The earliest known sauropod dinosaur. *Nature* 407:72–74.
- Calvo, J. O. and L. Salgado.** 1995. *Rebbachisaurus tessonei* sp. nov. a new Sauropoda from the Albian–Cenomanian of Argentina; new evidence on the origin of the Diplodocidae. *Gaia* 11:13–33.
- Carrano, M. T.** 2000. Homoplasy and the evolution of dinosaur locomotion. *Paleobiology* 26:489–512.
- Carrano, M. T., S. D. Samson and C. A. Forster.** 2002. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *J. Vert. Paleontol.* 22:510–534.
- Cooper, M. R.** 1981. The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: Its biology, mode of life and phylogenetic significance. *Occas. Pap., Natl. Mus. Monum. Rhodesia (Ser. B)* 6:689–840.
- 1984. A reassessment of *Vulcanodon karibaensis* Raath (Dinosauria: Saurischia) and the origin of the Sauropoda. *Palaeontol. Afr.* 25:203–231.
- Crompton, A. W. and J. Attridge.** 1986. Masticatory apparatus of the larger herbivores during the Late Triassic and Early Jurassic times. In: K. Padian, ed. *The beginning of the age of dinosaurs*. Cambridge: Cambridge Univ. Pr. pp. 223–236.
- Currie, P. J. and X. J. Zhao.** 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, Peoples Republic of China. *Can. J. Earth Sci.* 30:2037–2081.
- Farlow, J. O.** 1987. Speculations about the diet and digestive physiology of herbivorous dinosaurs. *Paleobiology* 13:60–72.
- Forster, C. A.** 1999. Gondwanan dinosaur evolution and biogeographic analysis. *J. Afr. Earth Sci.* 28:169–185.
- Fraser, N. C., K. Padian, G. M. Walkden and A. L. M. Davis.** 2002. Basal dinosauriform remains from Britain and the diagnosis of the Dinosauria. *Palaeontology* 45:79–96.
- Galton, P. M.** 1973. On the anatomy and relationships of *Efraasia diagnostica* (V. Huene) n. gen., a prosauropod dinosaur (Reptilia: Saurischia) from the Upper Triassic of Germany. *Palaeontol. Z.* 47:229–255.
- 1976. Prosauropod dinosaurs (Reptilia: Saurischia) of North America. *Postilla* 169:1–98.
- 1984a. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from the Knollenmergel (Middle Kueper, Upper Triassic) of Germany. I. Two complete skulls from Trossingen Würt. With comments on the diet. *Geol. Palaeontol.* 18:139–171.
- 1984b. An early prosauropod dinosaur from the Upper Triassic of Nordwürttemberg, West Germany. *Stuttg. Beitr. Naturkd. Ser. B.* 106:1–25.
- 1985a. Cranial anatomy of the prosauropod dinosaur *Sellosaurus gracilis* from the middle Stubensandstein (Upper Triassic) of Nordwürttemberg, West Germany. *Stuttg. Beitr. Naturkd. Ser. B.* 118:1–29.

- 1985b. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from the Knollenmergel (Middle Keuper, Upper Triassic) of Germany. II. All the cranial material and details of the soft-part anatomy. *Geol. Palaeontol.* 19:119–159.
- 1990. Basal sauropodomorpha—prosauropods. In: D. B. Weishampel, P. Dodson, and H. Osmólska, eds. *The Dinosauria*. Berkeley: Univ. California Pr. pp. 320–344.
- 2000. The prosauropod dinosaur *Plateosaurus* Meyer, 1837 (Saurischia: Sauropodomorpha). I. The syntypes of *P. engelhardti* Meyer, 1837 (Upper Triassic, Germany), with notes on other European prosauropods with “distally straight” femora. *Neues Jahrb. Geol. Paläontol. Abh.* 216:237–275.
- Galton, P. M. and R. T. Bakker.** 1985. The cranial anatomy of the prosauropod dinosaur “*Efraasia diagnostica*,” a juvenile individual of *Sellosaurus gracilis* from the Upper Triassic of Nordwürttemberg, West Germany. *Stuttg. Beitr. Naturkd. Ser. B.* 117:1–15.
- Galton, P. M. and J. Van Heerden.** 1985. Partial hindlimb of *Blikanasaurus cromptoni* n. gen. and n. sp., representing a new family of prosauropod dinosaurs from the Upper Triassic of South Africa. *Geobios* 18:509–516.
- 1998. Anatomy of the prosauropod dinosaur *Blikanasaurus cromptoni* (Upper Triassic, South Africa), with notes on other tetrapods from the lower Elliot Formation. *Palaeontol. Z.* 72:163–177.
- Galton, P. M. and P. Upchurch.** Basal sauropodomorpha—prosauropods. In: D. B. Weishampel, P. Dodson and H. Osmólska, eds. *The Dinosauria*. Berkeley: Univ. California Pr. In press.
- Gauthier, J.** 1986. Saurischian monophyly and the origin of birds. *Mem. Calif. Acad. Sci.* 8:1–55.
- Gilmore, C. W.** 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bull. U.S. Natl. Mus.* 110:1–154.
- 1936. Osteology of *Apatosaurus* with special reference to specimens in the Carnegie Museum. *Mem. Carnegie Mus.* 11:175–300.
- Gow, C. E.** 1990. Morphology and growth of the *Massospondylus* braincase (Dinosauria, Prosauropoda). *Palaeontol. Afr.* 27:59–75.
- Gow, C. E., J. W. Kitching and M. A. Raath.** 1990. Skulls of the prosauropod dinosaur *Massospondylus carinatus* Owen in the collections of the Bernard Price Institute for palaeontological research. *Palaeontol. Afr.* 27:45–58.
- He X., K. Li, K. Cai and Y. Gao.** 1988. [*Omeisaurus tianfuensis*—a new species of *Omeisaurus* from Dashanpu, Zigong, Sichuan]. *J. Chengdu Geol. Suppl.* 2:13–32. (In Chinese with English summary.)
- Heerden, J. Van and P. M. Galton.** 1997. The affinities of *Melanorosaurus*—a Late Triassic prosauropod dinosaur from South Africa. *Neues Jahrb. Geol. Paläont. Mh.* 1997:39–55.

- 
- Hitchcock, E.** 1865. A supplement to the ichnology of New England. Boston: Wright and Potter. 96 pp.
- Hoepen, E. C. N. van.** 1920a. Contributions to the knowledge of the reptiles of the Karoo Formation. 5. A new dinosaur from the Stormberg Beds. Ann. Transvaal Mus. 7:77–92.
- 1920b. Contributions to the knowledge of the reptiles of the Karoo Formation. 6. Further dinosaurian material in the Transvaal Museum. Ann. Transvaal Mus. 7:93–140.
- Holtz, T. R., Jr.** 1994. The phylogenetic position of the Tyrannosauridae: Implications for theropod systematics. J. Paleontol. 68:1100–1117.
- Huene, F. von.** 1914. Saurischia et Ornithischia triadica (“Dinosauria triadica”). Fossilium Catalogus. I. Animalia 4:1–21.
- 1926. Vollständige Osteologie eines Plateosauriden aus dem schwäbischen Trias. Palaeontol. Abh. 15:129–179.
- 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. Monogr. Geol. Palaeontol. (Ser. 1) 4:1–361.
- Jain, S. L., T. S. Kutty, T. Roychowdhury and S. Chatterjee.** 1979. Some characteristics of *Barapasaurus tagorei*, a sauropod dinosaur from the Lower Jurassic of Deccan, India. Proc. IV Int. Gondwana Symp. Calcutta 1:204–216.
- Janensch, W.** 1935–1936. Die Schädel der Sauropoden *Brachiosaurus*, *Barosaurus* und *Dicraeosaurus* aus den Tendaguruschichten Deutsch–Ostafrikas. Palaeontographica (Suppl. 7) 2:147–298.
- Kermack, D.** 1984. New prosauropod material from South Wales. Zool. J. Linn. Soc. Lond. 92:67–104.
- Langer, M. C.** 2001. *Saturnalia tupiniquim* and the early evolution of dinosaurs [dissertation]. Bristol, UK: University of Bristol. 415 pp.
- Basal Saurischia. In: D. B. Weishampel, P. Dodson and H. Osmólska, eds. The Dinosauria. Berkeley: Univ. California Pr. In press.
- Langer, M. C., F. Abdala, M. Richter and M. J. Benton.** 1999. A sauropodomorph dinosaur from the Upper Triassic (Carnian) of southern Brazil. C. R. Acad. Sci. Paris, Sci. Terre Plan. 329:511–517.
- Lee, M. S. Y.** 1996. Correlated progression and the origin of turtles. Nature 379:811–815.
- Lull, R. S.** 1912. The life of the Connecticut Trias. Amer. J. Sci. (Ser. 4) 33:397–422.
- Maddison, D. R. and W. P. Maddison.** 2000. MacClade 4.0 [computer program]. Sunderland, MA: Sinauer.
- Madsen, J. H., Jr.** 1976. *Allosaurus fragilis*: a revised osteology. Utah Geol. Mineral. Surv. Bull. 1091:1–163.
- Madsen, J. H., Jr., J. S. McIntosh and D. S. Berman.** 1995. Skull and atlas-axis complex of the Upper Jurassic sauropod *Camarasaurus* Cope (Reptilia: Saurischia). Bull. Carnegie Mus. Nat. Hist. 31:1–115.



- Madsen, J. H., Jr. and S. P. Welles.** 2000. *Ceratosaurus* (Dinosauria, Theropoda): a revised osteology. Misc. Pub. Utah Geol. Surv. 00-2:1–80.
- Marsh, O. C.** 1885. Names of extinct reptiles. *Am. J. Sci. (Ser. 3)* 29:169.
- 1889. Notice of new American Dinosauria. *Am. J. Sci. (Ser. 3)* 38:501–506.
- 1891. Notice of new vertebrate fossils. *Am. J. Sci. (Ser. 3)* 42:265–269.
- Molnar, R. E., S. M. Kurzanov and Z. Dong.** 1990. Carnosauria. In: D. B. Weishampel, P. Dodson, and H. Osmólska, eds. *The Dinosauria*. Berkeley: Univ. California Pr. pp. 169–209.
- Novas, F. E.** 1992. Phylogenetic relationships of the basal dinosaurs, the Herrerasauridae. *Palaeontology* 35:51–62.
- 1993. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *J. Vert. Paleontol.* 13:400–423.
- Ostrom, J. H. and J. S. McIntosh.** 1966. *Marsh's dinosaurs*. New Haven: Yale Univ. Pr. 388 pp.
- Padian, K.** 1997. Saurischia. In: P. J. Currie, and K. Padian, eds. *Encyclopaedia of Dinosauria*. London: Academic Pr. pp. 647–653.
- Pérez-Moreno, B. P., J. L. Sanz, A. D. Buscalioni, J. J. Moratalla, F. Ortega and D. Rasskin-Gutman.** 1994. A unique multitoothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature* 370:363–367.
- Raath, M. A.** 1972. Fossil vertebrate studies in Rhodesia: a new dinosaur (Reptilia: Saurischia) from near the Triassic–Jurassic boundary. *Arnoldia* 5:1–37.
- 1990. Morphological variation in small theropods and its meaning in systematics: evidence from *Syntarsus rhodesiensis*. In: K. Carpenter and P. J. Currie, eds. *Dinosaur systematics: approaches and perspectives*. Cambridge: Cambridge Univ. Pr. pp. 91–106.
- Rauhut, O. W. M.** 2000. The interrelationships and evolution of basal theropods (Dinosauria, Saurischia) [dissertation]. Bristol, UK: University of Bristol. 440 pp.
- Romer, A. S.** 1956. *Osteology of the reptiles*. Chicago: Univ. Chicago Pr. 772 pp.
- Salgado, L., R. A. Coria and J. O. Calvo.** 1997. Evolution of the titanosaurid sauropods. I: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana* 34:3–32.
- Santa Luca, A. P.** 1980. The postcranial skeleton of *Heterodontosaurus tucki* from the Stormberg of South Africa. *Ann. S. Afr. Mus.* 79:159–211.
- Sereno, P. C.** 1991. *Lesothosaurus*, “fabrosaurids,” and the early evolution of Ornithischia. *J. Vert. Paleontol.* 11:168–197.
- 1993. The pectoral girdle and forelimb of the basal theropod *Herrerasaurus ischigualastensis*. *J. Vert. Paleontol.* 13:425–450.
- 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. *Neue Jahrb. Geol. Paläontol. Abh.* 210:41–83.
- 1999. The evolution of dinosaurs. *Science* 284:2137–2147.

- Sereno, P. C. and A. B. Arcucci.** 1993. Dinosaurian precursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. J. Vert. Paleontol. 13:385–399.
- Sereno, P. C., A. L. Beck, D. B. Dutheil, H. C. E. Larsson, G. H. Lyon, B. Moussa, R. W. Sadlier, C. A. Sidor, D. J. Varricchio, G. P. Wilson and J. A. Wilson.** 1999. Cretaceous sauropods from the Sahara and the uneven rate of skeletal evolution among dinosaurs. Science 286:1342–1347.
- Sereno, P. C., D. B. Dutheil, M. Iarochene, H. C. E. Larsson, G. H. Lyon, P. M. Magwene, C. A. Sidor, D. D. Varricchio and J. A. Wilson.** 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. Science 272:986–991.
- Sereno, P. C., C. A. Forster, R. R. Rogers and A. M. Monetta.** 1993. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. Nature 361:64–66.
- Sereno, P. C. and F. E. Novas.** 1993. The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. J. Vert. Paleontol. 13:451–476.
- Steel, R.** 1970. Saurischia. Handb. Paläoherpetol. 14:1–87.
- Swofford, D. L.** 2002. PAUP\* (Phylogenetic analysis using parsimony) [computer program]. Version 4. Sunderland, MA: Sinauer.
- Thulborn, R. A.** 1972. The post-cranial skeleton of the Triassic ornithischian dinosaur *Fabrosaurus australis*. Palaeontology 15:29–60.
- Upchurch, P.** 1995. The evolutionary history of sauropod dinosaurs. Philos. Trans. R. Soc. Lond. Ser. B 349:365–390.
- 1998. The phylogenetic relationships of sauropod dinosaurs. Zool. J. Linn. Soc. 124:43–103.
- Weishampel, D. B. and L. Young.** 1996. Dinosaurs of the East Coast. Baltimore: Johns Hopkins Univ. Pr. 275 pp.
- Welles, S. P.** 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda). Osteology and comparisons. Palaeontographica A 185:85–180.
- White, T. E.** 1958. The braincase of *Camarasaurus lentus* (Marsh). J. Paleontol. 32:477–494.
- Wilson, J. A.** 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zool. J. Linn. Soc. 136:217–276.
- Wilson, J. A. and P. C. Sereno.** 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Soc. Vert. Paleontol. Mem. 5:1–68.
- Wyman, J.** 1855. Notice of fossil bones from the red sandstone of the Connecticut River Valley. Amer. J. Sci. (Ser. 2) 20:394–397.
- Yadagiri, P.** 2001. The osteology of *Kotasaurus yamanpalliensis*, a sauropod dinosaur from the Early Jurassic Kota Formation. J. Vert. Paleontol. 21:242–252.
- Yates, A. M.** 2003a. A new species of the primitive dinosaur, *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. J. Systematic Palaeontol. 1:1–42.

---

—2003b. The species taxonomy of the sauropodomorph dinosaurs from the Löwenstein Formation (Norian, Late Triassic) of Germany. *Palaeontology* 46:317–337.

**Young, C. C.** 1941a. A complete osteology of *Lufengosaurus huenei* Young (gen. et sp. nov.). *Palaeontol. Sinica* (Ser. C.) 7:1–53.

—1941b. *Gyposaurus sinensis* (sp. nov.), a new Prosauropoda from the Upper Triassic Beds at Lufeng, Yunnan. *Bull. Geol. Soc. China* 21:205–253.

—1951. The Lufeng saurischian fauna in China. *Palaeontol. Sinica* (Ser. C) 134:1–96.

**Zhang, Y.** 1988. [The Middle Jurassic dinosaur fauna from Dashanpu, Zigong, Sichuan: sauropod dinosaurs (1) *Shunosaurus*]. Chengdu, China: Sichuan Pub. House Sci. Technol. 89 pp. (In Chinese with English summary.)

